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THE QUARTERLY REVIEW of BIOLOGY



A RE-EXAMINATION OF THOREAU'S "WALDEN"

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INTRODUCTION

WHEN we regard Thoreau simply as an observer or as a natural historian," says Burroughs (1), "there have been better, though few so industrious and persistent. He was up and out at all hours of the day and night, and yet he saw and recorded nothing new. It is quite remarkable. . . . He has added no new line or touch to the portrait of bird or beast that I can recall. . . . He had not the detective eye of the great naturalist. . . . To the last, his ornithology was not quite sure, not quite trustworthy."

In this paper I propose to show that, however untrustworthy Thoreau's ornithology may have been, his contribution to at least one natural science, limnology, was original and genuine.

The bulk of Thoreau's limnological observations are set down in *Walden*, although some very important material is confined to his *Journal* and remained unpublished until long after his death. These notes, like his other records of natural history, are fragmentary and discursive, conforming to no methodical program of study or presentation. Nevertheless they have a great intrinsic interest for the ecological reader, and a renewed acquaintance with *Walden* prompted a journey to that lake, the results of which are described below.

The field observations were made on August 6, 1939, during a brief holiday from the Biological Survey of Connecticut lakes then being conducted by the Connecticut State Board of Fisheries and

Game. The technical and analytical methods used are referred to elsewhere (2). I am deeply indebted to Professor G. E. Hutchinson for invaluable advice and encouragement, for investigating the history of the discovery of thermal stratification, and for the collection of a water sample from Walden Pond on July 16, 1939. My wife, Georgiana Baxter Deevey, rendered indispensable assistance in the field and in the laboratory. Facilities and equipment were generously provided by the Osborn Zoological Laboratory, and acknowledgment is made to the officials of the Rice Institute Library and the Mirabeau B. Lamar Library of the University of Texas for many courtesies. The manuscript has been read by Dr. A. D. McKillop, of The Rice Institute, and by Dr. Henry Seidel Canby, editor of *The Saturday Review of Literature*.

LIMNOLOGY OF WALDEN POND

Location and hydrography

The lake on whose banks Thoreau spent two of the most profitable years of his life (from July 4, 1845 to September 6, 1847) is in the town of Concord, Massachusetts, where he was born. The physiography of the Concord region bears witness to the activity of the Pleistocene ice sheets, as may be seen by inspection of the U. S. Geological Survey topographic map (Framingham quadrangle). Fig. 1, based on part of this map, shows the disorganized stream pattern and abundant undrained depressions so characteristic of a glaci-

ated landscape. Walden Pond, a seepage lake, is situated at an elevation of about 140 feet. The fact that the lake fills the bottom of a closed basin whose walls rise steeply nearly forty feet above the shore line suggests that the concavity is of kettle origin; this hypothesis is supported by the morphometry of the lake, but time did not permit the making of any geomorphic studies.

visit, it was essential to make another. The procedure adopted was the one used in limnological surveys of Connecticut lakes (2); an aerial photograph was obtained from the Fairchild Aerial Surveys, Incorporated, and the outline traced. Lines were chosen between conspicuous points on the lake shore, and soundings made at intervals of ten oar strokes, using a lead weight lowered from a

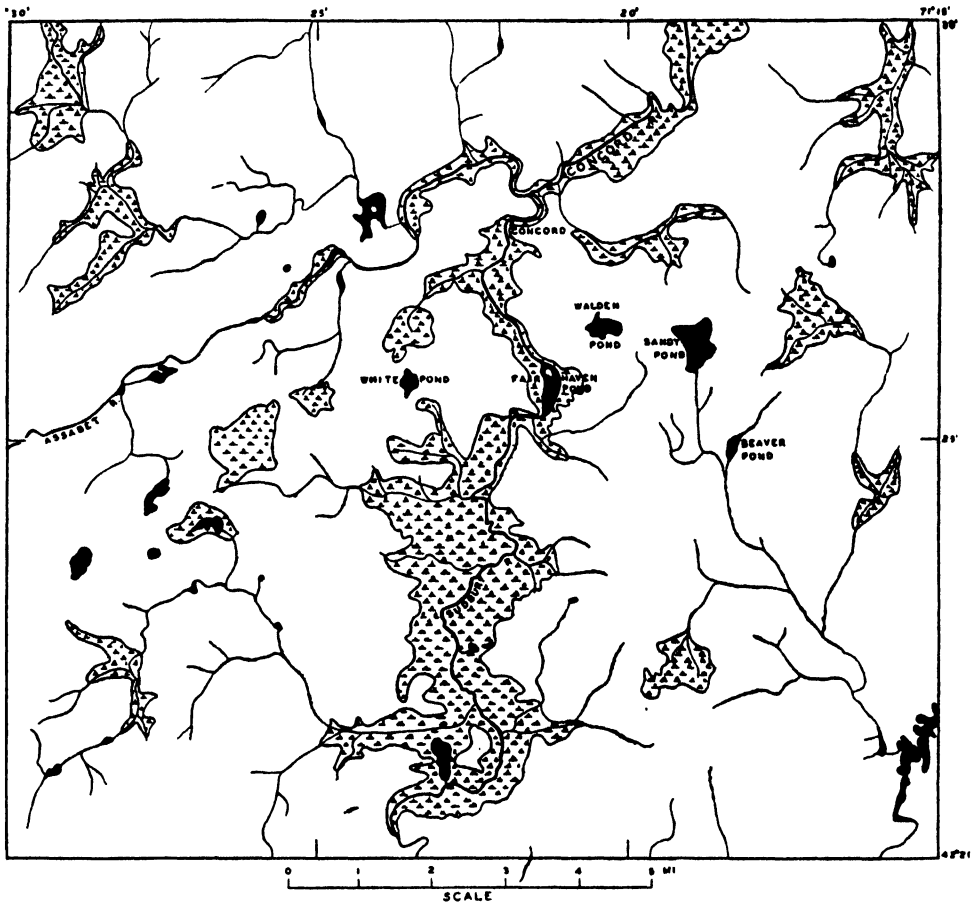


FIG. 1: SKETCH MAP OF THOREAU'S "LAKE DISTRICT," BASED ON U. S. GEOLOGICAL SURVEY TOPOGRAPHIC MAP (FRAMINGHAM QUADRANGLE)

Because he was amused by the local legend that Walden Pond is of infinite depth, and to satisfy his highly individual curiosity about the lake, Thoreau was at pains to sound it "with compass and chain," in the winter of 1846, and plotted his results on an outline map. This map, which is reproduced in Fig. 2 by courtesy of the Huntington Library, was published in the first edition of *Walden* but was withdrawn from later issues. As this map was inaccessible at the time of my

hand winch on music wire. The lake is small and well protected from wind, and so this method may be expected to give unusually reliable results. The map is shown in Fig. 3.

The similarity between the two maps is in some respects so close as to be startling (provided it is realized that, by modern convention, Thoreau's map is "upside down"). It is certain that the outline map used by Thoreau was his own, for a county map published by H. F. Walling in 1852

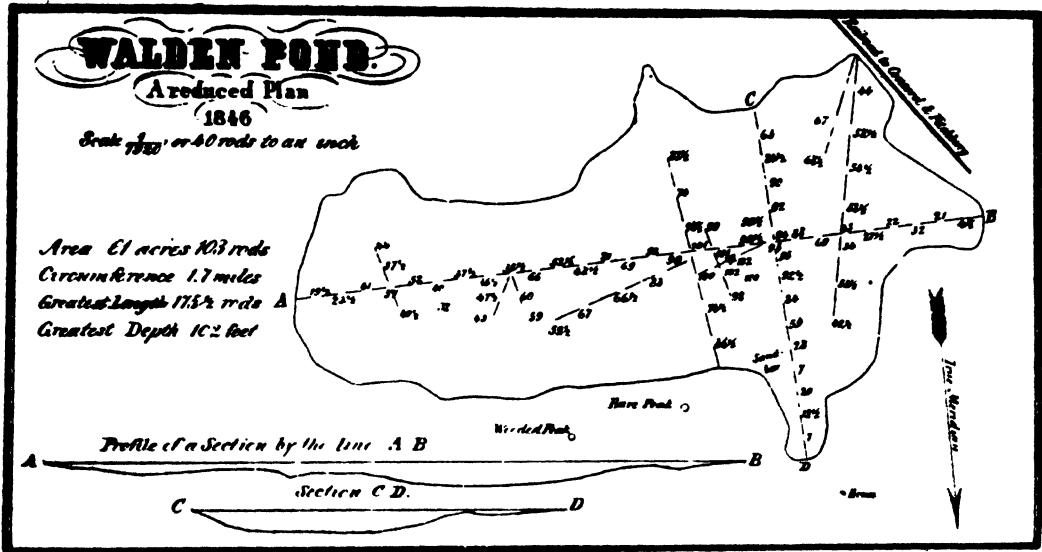


FIG. 2. THOREAU'S MAP OF WALDEN POND, REPRODUCED FROM THE FIRST EDITION OF "WALDEN" BY COURTESY OF THE HUNTINGTON LIBRARY, SAN MARINO, CALIFORNIA

Notice that by modern convention the map is "upside down."

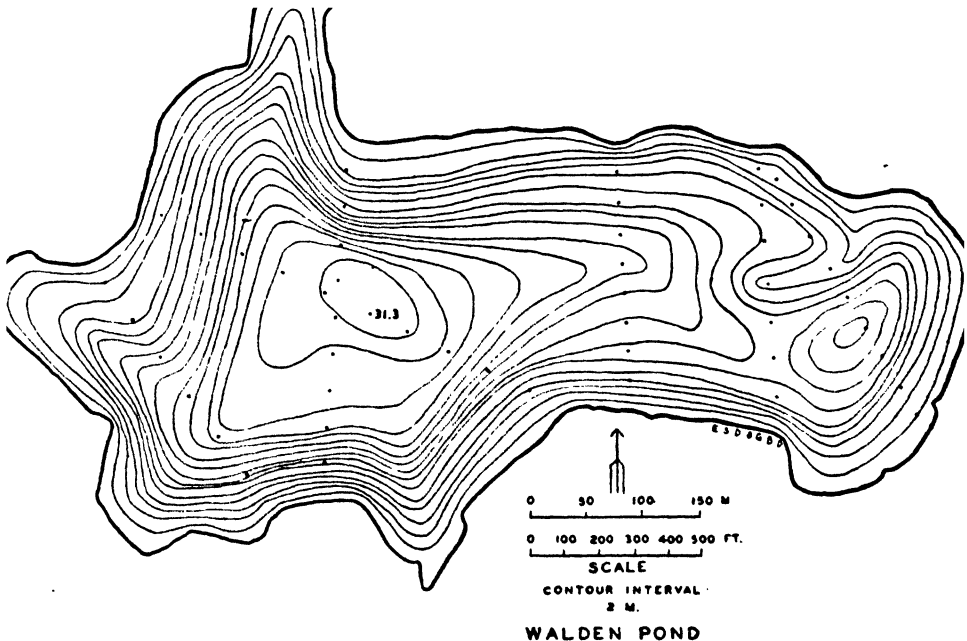


FIG. 3. BATHYMETRIC MAP OF WALDEN POND, FROM DATA OBTAINED AUGUST 6, 1939

gives credit for the outlines of Walden and White Ponds to "H. D. Thoreau, Civil Engineer" (3). The aerial survey map is almost precisely con-

gruent with Thoreau's; moreover, the area of the lake as given by him, 24.98 hectares, is remarkably close to that computed from my map, 24.82

hectares. The agreement may be deceptive, as a slight error is inherent in the determination of the scale of the aerial photograph, but the comparison offers valuable testimony to Thoreau's competence as a surveyor.

With the entire winter at his disposal, Thoreau (4) had time to make over one hundred soundings, seventy-five of which are shown on his published map; only forty-nine were made in 1939. Morphometric comparisons based on these soundings are very instructive, not only because they betray Thoreau's inexperience in such work, but for the

TABLE 1
Morphometric data for Walden Pond
1939

CONTOUR m	AREA WITHIN m ²	AREA BETWEEN m ²	VOLUME m ³
0	248,200	25,600	470,600
2	222,600	21,900	423,200
4	200,700	20,100	381,100
6	180,600	19,300	341,500
8	161,300	16,600	305,800
10	144,700	20,100	269,100
12	124,600	20,900	228,000
14	103,700	17,100	190,000
16	86,600	16,100	156,900
18	70,500	12,000	128,900
20	58,500	10,100	106,800
22	48,400	9,200	87,500
24	39,200	10,300	74,500
26	28,900	15,000	41,900
28	13,900	9,800	17,100
30	4,100		1,250
			3,224,150

Mean depth..... 13.0 m.
Perimeter..... 2,535 m.
Shoreline development..... 1.75
50 per cent of volume covered by 6-m.
contour.

insight they give into the reliability of the more convenient method. The modern limnologist requires a bathymetric map in order to compute areas and volumes at different depths. For the determination of these values soundings in the deepest water are less important than those in shallow, since the volume covered by the deeper isobaths is small. In emphasizing the depths of the lake basin Thoreau neglected the shallows, which can be defined with greater confidence from the later map; when he said (5) "there is a bar across the entrance of our every cove, or particular inclina-

tion; each is our harbour for a season," he either exaggerated the probable extent of the bars in question or referred to unpublished soundings. Inspection of all available data indicates that the subsidiary basin shown by Thoreau's profile AB is in reality an irregular extension of the 20-meter contour to the southeast beyond the form shown in Fig. 3. Areas calculated from a map incorporating all soundings differ from those based on the 1939 map by a maximum of 29.6 per cent; this figure represents the difference between the 30-meter contours, which are almost negligibly small, and the maximum discrepancy for contours above 28 meters is 8.1 per cent. Values for lake volume estimated from the two maps differ by only 0.6 per cent.

It is interesting that the maps agree upon the maximum depth, which Thoreau found to be 31.1 meters, and I found to be 31.3 meters. As variations of the lake level amounting to two meters or more are known to occur (6), this approximation may be put down in part to coincidence, but the two soundings were made at almost exactly the same spot. Thoreau (7) noted that this point marks the intersection of the lines of maximum length and breadth, and speculated on the possibility that this phenomenon is a general one.

The morphometric data, calculated from planimeter measurements of the 1939 map, are set forth in Table 1.

Temperatures

Thoreau frequently had recourse to a thermometer in answering his questions about nature, and his knowledge of physics enabled him to make some sound inferences about the melting of lakes in the spring. He noted the rise in water temperature beneath the ice over shoals, ascribed it to back-radiation from the bottom, and correctly deduced that the difference in time of melting between Walden and Sandy Pond arises from their difference in depth (8). The natural history of ice has seldom been so glowingly described as in the pages of *Walden*. His most significant physical observations, however, may be found in the later *Journal* (9), where under date of August 22, 1860, he records the discovery of the thermal stratification of Walden Pond. The method employed was crude; he filled a bottle with water from the surface, stoppered it, and after lowering it to the bottom, allowed half an hour for the establishment of thermal equilibrium. The temperature was re-

corded after raising the bottle. Unfortunately only two determinations, at 50 and 100 feet, were thus made, and on the mistaken but natural assumption that the fall in temperature with depth was linear he calculated the average decrease to be one degree Fahrenheit in five feet (10). The biological importance of his discovery did not escape Thoreau, who remarks, "How much this varied temperature must have to do with the distribution of fishes in it! The few trout must oftenest go down below in summer."

Because of its unusual depth and sheltered situation Walden Pond has an exceptionally cold hypolimnion; the temperature at 30 meters in August,

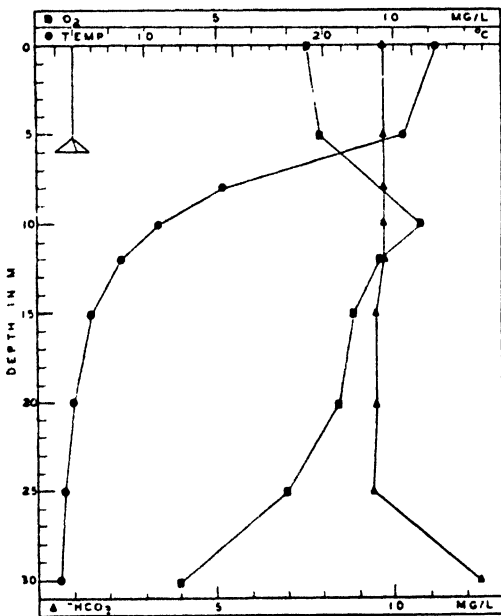


FIG. 4. LIMNOLOGICAL DATA FOR WALDEN POND, AUGUST 6, 1939

1939, was 5.26 degrees Centigrade, as measured with a reversing thermometer. In other respects the temperature curve shown in Fig. 4 is normal. Walden, however, acquires a surprising amount of heat during the summer season. The annual heat budget can not be calculated without a series of winter temperatures, but the wind-distributed heat, or summer heat income (assuming homothermy at 4°C.) amounts to 17,300 calories per square centimeter of lake surface. This value is considerably in excess of any observed in Connecticut lakes; Wononscopomuc Lake, which closely resembles Walden in depth, has a summer heat income of only 10,800 cal. per sq. cm., and the

largest value observed was 12,800 cal. per sq. cm. in the somewhat shallower but larger East Twin Lake.

None of these lakes is of the first thermal class, in which Birge (11) placed lakes "whose size and depth are such as to permit [them] to acquire the maximum amount of heat possible under the weather conditions of the season." Such lakes in the eastern United States have summer heat incomes of at least 24,000 cal. per sq. cm. and annual heat budgets between 30,000 and 40,000 cal. per sq. cm. Tressler and Bere (12) have recently shown that the limits of area and depth set by Birge for first-class lakes are too high; Sylvan Lake, New York, with an area of 50.6 hectares, a maximum depth of 38 meters, and a mean depth of 21.6 meters, had a summer heat income of 24,000 cal. per sq. cm. in 1936. These figures must be regarded as the lower limits in the present state of our knowledge, and it is clear that Walden does not quite attain this rank, although it approaches it more closely than any other small New England lake yet studied.

Transparency

One of Walden's major charms for Thoreau lay in its exceptional clearness—he found that "the water is so transparent that the bottom can easily be discerned at the depth of twenty-five to thirty feet" (13). It was impossible to corroborate this determination in 1939, as the Sécchi disc was not lowered until late in the afternoon, in a part of the lake made noticeably turbid by the activities of nearly a thousand Sunday bathers. The reading of 6 meters is obviously not reliable under these circumstances, but that the lake is unusually transparent is made certain by the fact that living specimens of *Fontinalis* came up with the sounding weight from depths as great as 15.7 meters. This moss is presumably the "bright green weed . . . brought up on anchors even in midwinter" (14). Thoreau also records aquatic vegetation from below 12 meters in White Pond, and his queried identification (15) of the plant as *Nitella gracilis* is no doubt substantially correct.

Observations of much greater depths for "rooted" plants are of course on record; Hasler (16) has recently noted water mosses from 120 meters in Crater Lake, Oregon, but casual records indicate a maximum depth of only 12 meters for the growth of vegetation in Connecticut lakes.

The color of the water is 5 (on the U. S. G. S.

scale) throughout the lake except in the bottom layer; this lack of appreciable contamination by allochthonous organic matter is largely responsible for the high transparency (17).

Nutrient content

The mean of two determinations, in July and August, 1939, shows the total phosphorus content of the surface waters of Walden to be very low, 11.5 mg. per cu. m. This condition may be partly due to the fact that the lake is fed solely by ground water, but the regional lithology is such that Concord lakes may be expected to resemble those of the Connecticut highlands in being oligotypic for phosphorus. The above figure is below the mean content of forty-nine Connecticut and New York lakes, and falls between the regional means for the Eastern and Western Highlands (2). The soluble phosphorus was not measured.

The mean surface nitrate content is 20.5 mg. per cu. m. In default of more extensive data this figure has no great significance, as the supply of available nitrogen fluctuates through wide limits during the summer. The potential nitrogen endowment of a lake can sometimes be estimated from the winter nitrate, but no winter analyses are available for Walden.

Biological productivity and oxygen deficit

That Walden is a relatively unproductive lake was appreciated by Thoreau, who observed the scanty crop of littoral vegetation, the absence of organic sediment except in the deepest water (where he correctly attributed its existence to decomposing forest leaves), and the "purity" of the water. He also realized that food chains are thus affected, "you think that they must be ascetic fish that find a subsistence there" (18); and he points out that the larger but comparatively shallow Sandy Pond (Flint's Pond) supports an abundance of aquatic vegetation, is "not remarkably pure," and "is more fertile in fish" (19).

Walden water is indeed "pure" in respect to its plankton content. Plankton counts have not been made, but two analyses of the chlorophyll present in the surface water give a mean value of 3.64 mg. per cu. m. (20), and the Forel-Ule color of the lake is 3. Walden thus closely resembles the lakes of the Eastern Highland of Connecticut in its summer phytoplankton crop (2). The total seston has been estimated gravimetrically from the residue after filtration through a 35-second

membrane filter, and found to be extremely low, 0.5 mg. per liter; the amount of ash in this amount of seston was not detectable, so that the same figure represents the organic matter in the seston. No quantity as low as this has been recorded from twenty-four Connecticut and New York lakes, but Birge and Juday (21) report values as low as 0.23 mg. per l. for centrifuge plankton, which is comparable to the membrane filter residue, in north-eastern Wisconsin lakes. Expressed on an areal basis, the observed plankton crop amounts to 0.65 mg. per sq. cm., or 65 kilos per hectare, but this can not safely be taken as an average productivity.

The oxygen curve, as shown in Fig. 4, is essentially of the oligotrophic type; the total oxygen content of the hypolimnion is nearly as great as that of the epilimnion, the ratio O_2H/O_2E being 0.73. The curve is further characterized by a maximum in the thermocline. The latter feature gives additional evidence of the transparency of the lake, since such maxima are commonly produced by the photosynthetic activity of phytoplankton organisms concentrated below the epilimnion in the hydrodynamically more stable thermocline, and are not found in lakes in which the compensation point normally lies at a higher level (22).

The oligotrophic form of the curve may with some justice be attributed to the relatively large volume of the hypolimnion, and it is necessary to calculate the areal hypolimnetic oxygen deficit in order to evaluate the fundamental productivity of the lake from the oxygen data (23). Taking the hypolimnion as beginning at 10 meters, and assuming the vernal circulation to have begun on April 1 (Thoreau's average date (24)), the oxygen deficit observed on August 6 appears to have been generated at the rate of 0.0173 mg. per sq. cm. of hypolimnion surface per day, or 0.52 mg. per sq. cm. per month. This single determination of the increment is not altogether reliable, since estimates of the deficit in small lakes, particularly in those of unusual transparency, tend to be minimal (25); but when taken in conjunction with the low standing crop of plankton, the calculation indicates that Walden is a mesotrophic lake. This fact might have been predicted from the geologic similarity between the Massachusetts upland and the Connecticut highlands. Walden, like the lakes of the latter provinces, is unproductive by comparison with those of southeastern Wisconsin (23), or the Connecticut Valley Lowland (2), but

more productive than the mountain lakes of Norway (26).

Alkalinity and iron

The surface bicarbonate content of Walden (9.7 mg. per l) is very low, as might be expected in a seepage lake, and this fact serves to rank it as a soft-water lake. A statistical examination of Connecticut lakes makes it seem highly probable that low alkalinity has no adverse effect on phytoplankton production (2).

Walden resembles other mesotrophic and oligotrophic lakes in the uniform character of its alkalinity curve (Fig. 4); eutrophic lakes (for example, Linsley Pond, Connecticut) frequently show a rise in bicarbonate content in the hypolimnion, due to the acquisition of ferrous and other non-alkali bicarbonates from the mud and their delivery to the open water by density currents (27). The low content of total iron, as shown in

TABLE 2
Total iron

DEPTH	Fe
0 m.	0.045 mg./l
20	0.00
25	0.00
30	0.30

Table 2, also demonstrates that this process is quantitatively unimportant in Walden.

Bottom fauna

Although the examination of Walden was made too early in the season to obtain limiting values of the oxidation-reduction potential, the above facts enable one to affirm that the typical Chironomid larva of the profundal zone should be either a species of *Tanytarsus* or the "mesotrophic *Chironomus*" found in similar lakes in Connecticut (28). Analysis of two Ekman bottom samples from 28.2 and 23 meters indicates that the character-form is "mesotrophic *Chironomus*." This larva lacks the ventral blood gills regarded as characteristic of the genus *Chironomus* by Lenz (29), and is known to occur on the bottoms of lakes showing values of the redox potential intermediate between those of typical *Tanytarsus* and typical *Chironomus* lakes (28).

Reliable conclusions as to the abundance of bottom organisms can not be drawn from the two

samples taken, but the data appear to reflect a low to moderate benthic productivity. In addition to *Chironomus*, all instars of which were present in the 23-meter sample, the observed fauna comprises several Chironomid larvae of the sub-family Tanypodinae, a few larvae and pupae of *Chaoborus*, and some Tubificid Oligochaets. Cyst capsules characteristic of the Harpacticoid copepod *Conthocamptus staphylinoides* were frequent (30), but none appeared to be occupied. No molluscs were encountered, nor were any *Tanytarsus* tubes found.

The sediment of the profundal zone is a typical ooze, and the washed samples contain a high proportion of fragments from the leaves of deciduous forest trees. The presence in the residues of a small amount of carbon, evidently derived from the soot of passing locomotive engines, would have been interesting but scarcely surprising to Thoreau, who resented the intrusion of the nearby railroad.

Limnological summary

Walden Pond, an unusually deep soft-water seepage lake in the Massachusetts upland, is exceptionally transparent, acquires a large amount of heat during the summer season, and closely resembles the lakes of the Connecticut highlands in its low phosphorus content, low plankton crop, and generally low biological productivity. The oxygen curve reflects an oligotrophy (or mesotrophy) which is in part of morphometric and in part of edaphic character. The quantitatively moderate bottom fauna is dominated by "mesotrophic *Chironomus*" larvae. Many limnologically important facts about Walden were first stated by Thoreau.

THOREAU'S PLACE IN SCIENCE

Thoreau's supremacy as an observer of nature among American men of letters has never been seriously questioned since the publication of *Walden*, and even John Burroughs, who complains of the lack of originality in his master's ornithology, finds much to admire in his descriptions. It is strange, therefore, that most of his critics, and, one must suppose, most of his readers, have confined their attention to other facets of his many-sided genius. Leaving aside the other biographies and critical studies, it is sufficient to recall that Canby, perhaps the most discerning and certainly the most widely-informed of Thoreau's biographers, finds his present-day importance to lie chiefly in his moral criticism (31).

It is true, as Canby says, that Thoreau speaks with a homely and original eloquence to readers of many sorts, so that many biographies of the Yankee "hermit" could be written, each with a different and defensible point of view. The biologist, however, must be expected to feel his attraction principally in the sphere of his natural science, and to assess his significance from the lectern of special knowledge.

It has been shown that Thoreau's curiosity was unusually fruitful when directed toward lakes; it is remarkable that this fact appears to have escaped the notice, not only of historians of limnology (32), but of his scientific contemporaries. Limnology, as a separate science, is usually considered to begin with the work of Forel, in 1868, and, except for scattered reports primarily of a taxonomic nature, American limnology was not properly established until after 1890. Thoreau's observations, at least those embodied in *Walden*, were published in 1854, so that the Concord individualist may with justice be called the first American limnologist. His independent discovery of thermal stratification remained in manuscript until 1906, but in any case was antedated by the work of DeSaussure, de la Bèche, Brunner and Simony, who had elucidated the fundamental principles of the temperature distribution in lakes during the latter third of the eighteenth and first half of the nineteenth centuries (33).

The neglect of Thoreau's writings by the scientific world is undoubtedly due to a pardonable distrust of his philosophy. Although he was a corresponding member of the Boston Society of Natural History, an enthusiastic botanist, and a friend of Louis Agassiz, Thoreau never thought of himself as a scientist, but rather as "a mystic, a transcendentalist, and a natural philosopher to boot" (34). According to Sanborn, while Agassiz enjoyed Thoreau's society, "the poet avoided the man of science, having no love for dissection" (35). His works abound in impatient references to the desiccated concepts and vestigial insight of science; in a revealing passage in his *Journal* he rejects what would now be called "phototropism" as an explanation for the turning of plants toward the sun, preferring a more mystical causality (36). "I hate museums," he says, "they are the catacombs of nature" (37). "The inhumanity of science concerns me, as when I am tempted to kill a rare snake that I may ascertain its species. I feel that this is not the means of acquiring true knowledge" (38). "What sort of science is that which enriches the understanding, but robs the

imagination? . . . Just as inadequate to a pure mechanic would be a poet's account of a steam engine" (39). "Which are the truest, the sublime conceptions of Hebrew poets and *seers*, or the guarded statements of modern geologists, which we must modify or unlearn so fast" (40)? Such sentiments show as clearly as his more intricate paragraphs Thoreau's largely unconscious kinship with German romanticism (41); they represent a reverberation of *Naturphilosophie*.

Although his thought is steeped in an idealism which the modern biologist can only regard as unfortunate, Thoreau's wide-ranging observation embraced much that was new, and his reflections frequently are cautious, objective, and ingenious; he was a genuine scientist, if only at intervals. As he was a "self-appointed inspector" of the Concord environment, his science as a rule is more distinguished for its scope than for its profundity. His researches led him into such diverse disciplines as plant ecology, systematic botany, animal behavior, ichthyology, anthropology, and geomorphology, in addition to limnology. Yet his versatility, even though hampered by a meager technical facility, did not result in a futile expenditure of his energies.

Thoreau's botany has usually been regarded as his chief claim to scientific eminence. But it is as a plant ecologist, not as a systematist, that this claim is justified. It seems strange that he first made the acquaintance of *Rhododendron nudiflorum* in 1853 (42); in reading the *Philosophia Botanica* of Linnaeus, however, his interest was principally aroused by the ecological classification of plant habitat (43). In one of the last lectures delivered before his death he spoke to the Middlesex Agricultural Society on "The Succession of Forest Trees"; though he overemphasized the reversibility of plant succession, having observed that pine forests usually succeed oak after cutting, his conclusions remain essentially unaltered after sixty years of intensive labor by competent botanists. His view of the dynamics of plant succession was not confined to short-term processes. He not only plumbed the depths of all the bogs known to him, realizing that they were merely senescent lakes, but correctly ascribed the formation of the floating mat to ericaceous shrubs as well as to *Sphagnum* (44). While Thoreau can not be said to have introduced the subject to science, it appears that no important studies of ecological succession were made in America for more than thirty years after his memorable lecture (45).

Many notes on forestry problems made after

the delivery of the lecture are incorporated in the *Journal*, and the last volume is notable for a remarkably acute investigation of the growth of the pitch pine (46). Thoreau appreciated fully the uses of tree-ring analysis, and although the growth curves constructed from his data appear to have remained in his head, he understood their value in ascertaining the most productive period in the life of a stand. It is probable that such studies were meant when he wrote to a correspondent, "if I were to live, I should have much to report on Natural History generally" (47).

These truly scientific observations, and many more of equally astonishing perception, were made by a "poet-naturalist," a disciple of Emerson, and an accepted member of the Concord coterie of transcendentalists. This paradox implies either that he was alternately scientist and mystic, or that being both, he was neither. It has been said that "if Emerson had not spoiled him, Thoreau would have made a good naturalist" (48). On the other hand, Canby expresses the opinion that after the years at Walden, Thoreau was increasingly drawn toward science, but that he was unfortunate in falling under the influence of Agassiz, a taxonomist (49). This view fails to do entire justice to the promulgator of the Glacial Theory, a superb naturalist whose thinking was no less philosophical than Darwin's (50). But at bottom Thoreau's scientific difficulties were of his own contriving, and it is unfair to suggest that he was subverted by anyone. If he mistook the means of scientific observation for its end, and thus remained blind to the advantages of technique, the fault lay partly in the formal curriculum of Harvard College, and partly in his innate distaste for empiricism. Were all such speculations not idle, one might agree with Canby that the world lost a first-rate scientist when Thoreau did not go to Yale, and thus failed to meet Benjamin Silliman.

It is clear, however, that Thoreau's philosophy underwent a change as the habit of observation became more fixed, and the later *Journal* reveals a mind increasingly preoccupied with nature for its own sake and emancipated from the search for an esoteric truth. This alteration is merely implicit; murmurs of the Over-Soul can be detected as plainly in the later writings as in the earlier, and as late as 1860 he announced "I am in the lecture field—but my subjects are not *scientific*—rather transcendental and aesthetic" (51). But such statements decrease in number toward the end of his life, and it seems likely that only his premature death obstructed a "working synthesis of science

and Transcendentalism" (52). In its diversion from occultism toward nature Thoreau's career offers a refreshing contrast to that of many able scientists. Canby contends that the *Journal* represents the unfinished note-sheets for a monumental contribution to geography, based on an exhaustive study of the natural history of man in Concord (53). This task, as Thoreau conceived it, was superhuman, and scarcely to be accomplished by a man who died at forty-four.

But if it be admitted that Thoreau's mysticism is indefensible, and his science handicapped by his unwillingness to use a valid methodology, his works can nevertheless appeal to a wide biological audience. In his vigorous description of natural phenomena Thoreau stands almost without a peer, and modern biological literature would gain much by emulation of his style and diction. Science has devised no substitute for the charm of his locution, as when he says "thus in the course of ages the rivers wriggle in their beds, till it feels comfortable under them" (54), or speaks of the "maple succeeding because it does not mind a wet foot" (55). A pearl is for him "the hardened tear of a diseased clam, murdered in its old age" (56), and he discusses the "solvency of sand banks" (57). In a noteworthy example of his wit, he pays his respects to those who "believe in the bottomlessness of a pond without taking the trouble to sound it"; "Some who have lain flat on the ice for a long time, looking down through the illusive medium, perchance with watery eyes into the bargain, and driven to hasty conclusions by the fear of catching cold in their breasts, have seen vast holes 'into which a load of hay might be driven,' if there were anybody to drive it, the undoubted source of the Styx and entrance to the Infernal Regions from these parts. Others have gone down from the village with a 'fifty-six' and a wagon load of inch rope, but yet have failed to find any bottom; for while the 'fifty-six' was resting by the way, they were paying out the rope in the vain attempt to fathom their truly immeasurable capacity for marvellousness" (58).

Thoreau's pages are made vivid by such sentences, and although many passages have become classic, for example those dealing with his encounter with the woodchuck and the computation of the bullfrogs, and have found their way into compilations, the best of him, after *Walden*, is still to be found only in the *Journal*. No natural scientist need be so offended by Thoreau's perverse misunderstanding of the function of science as to neglect him. While the Yankee philosopher,

largely by accident and in spite of his philosophy, occasionally surpassed his more stolid contemporaries at their own profession, the modern reader will rank him with Sir Thomas Browne and W. H.

Hudson as a highly gifted amateur, whose scientific achievements are not to be despised because they were intermittent, and related in imaginative prose.

LIST OF LITERATURE

References to Thoreau's "Journal" and to "Walden" are to the *Walden Edition* of his works (*Boston and New York*, Houghton Mifflin Co., 1906) in 20 volumes, of which Volumes 7 to 20 contain the "Journal," edited by Bradford Torrey.

- (1) BURROUGHS, JOHN: Henry D. Thoreau. In *Indoor Studies*. London, J. M. Dent and Co., 1895, pp. 1-42.
- (2) DEEVEY, E. S.: Limnological studies in Connecticut. V. A contribution to regional limnology. *American Journal of Science*, Vol. 238, pp. 717-741, 1940.
- (3) Note by H. W. GLEASON, appended to map in Thoreau's Journal, Vol. 20, following end of text.
- (4) Walden, (Walden edition, Volume 2), p. 319.
- (5) *Ibid.*, p. 321.
- (6) *Ibid.*, p. 201.
- (7) *Ibid.*, p. 319.
- (8) *Ibid.*, p. 331.
- (9) Journal, Vol. 20, p. 60.
- (10) *Ibid.*, p. 66.
- (11) BIRGE, E. A.: The heat budgets of American and European lakes. *Trans. Wisconsin Acad. Sci., Arts, and Lett.*, Vol. 18, pp. 1-47, 1915.
- (12) TRESSLER, W. L., and R. BERE: A limnological study of some lakes in the lower Hudson area. *N. Y. State Cons. Dept., Ann. Rep.*, Vol. 26 (Suppl.); *Dept. Biol. Surv.*, No. 11, pp. 249-263, 1937.
- (13) Walden, p. 197.
- (14) *Ibid.*, p. 199.
- (15) Journal, Vol. 9 (March 11, 1852).
- (16) HASLER, A. D.: Fish biology and limnology of Crater Lake, Oregon. *Jour. Wildlife Management*, Vol. 2, pp. 94-103, 1938.
- (17) JUDAY, C., and E. A. BIRGE: The transparency, the color, and the specific conductance of the lake waters of northeastern Wisconsin. *Trans. Wisconsin Acad. Sci., Arts, and Lett.*, Vol. 28, pp. 205-259, 1933. See also Deevey, E. S., Reference 2.
- (18) Walden, p. 197.
- (19) *Ibid.*, p. 216.
- (20) RILEY, G. A.: The measurement of phytoplankton. *Int. Rev. ges. Hydrobiol. u. Hydrogr.*, Bd. 36, s. 371-373, 1938.
- (21) BIRGE, E. A., and C. JUDAY: Particulate and dissolved organic matter in inland lakes. *Ecol. Mon.*, Vol. 4, pp. 440-474, 1934.
- (22) YOSHIMURA, S.: Stratification of dissolved oxygen in a lake during the summer stagnation period. *Int. rev. ges. Hydrobiol. u. Hydrogr.*, Bd. 38, s. 441-449, 1939.
- (23) HUTCHINSON, G. E.: On the relation between the oxygen deficit and the productivity and typology of lakes. *Ibid.*, Bd. 36, s. 336-355, 1938.
- (24) WALDEN, pp. 330, 334.
- (25) RILEY, G. A.: Limnological studies in Connecticut. I. General limnological survey. *Ecol. Mon.*, Vol. 9, pp. 53-66, 1939.
- (26) STRØM, K. M.: Limnological observations on Norwegian lakes. *Arch. Hydrobiol.*, Bd. 21, s. 97-124, 1930.
—: Feforvatn. A physiographical and biological study of a mountain lake. *Ibid.*, Bd. 22, s. 491-536, 1931.
—: Lilla Le. A preliminary survey of a remarkable lake. *Geograf. Ann.*, 1932, pp. 259-272.
- (27) HUTCHINSON, G. E.: Limnological studies in Connecticut. IV. The mechanisms of intermediary metabolism in stratified lakes. *Ecological Monographs*, Vol. 11, pp. 21-60, 1941.
- (28) HUTCHINSON, G. E., E. S. DEEVEY, and A. WOLLACK: The oxidation-reduction potentials of lake waters and their ecological significance. *Proc. Nat. Acad. Sci.*, Vol. 25, pp. 87-90, 1939.
- (29) LENZ, F.: Chironomidenpuppen und Larven. Bestimmungstabellen. *Deutsch. Entomol. Zeit.*, 1921, s. 148-162.
- (30) MOORE, G. M.: A limnological investigation of the microscopic benthic fauna of Douglas Lake, Michigan. *Ecol. Mon.*, Vol. 9, pp. 537-582, 1939.
- (31) CANBY, H. S.: Thoreau. *Boston*, Houghton Mifflin Co., 1939, 508 pp.
- (32) WELCH, P. S.: Limnology. *New York and London*, McGraw-Hill, 1935, 471 pp.
- (33) DE SAUSSURE, H.-B.: Voyages dans les Alpes. *Geneva*, 1779-1796. (Especially I, Ch. 2, and V., Chap. 2).
DE LA BÈCHE, H. T.: On the depth and temperature, etc. *Bibliothèque Universelle des Sciences, Belles-Lettres, et Arts*, T. 12 (Sci. et Arts), pp. 118-126. *Geneva*, 1819.
BRUNNER, C.: Recherches sur la température du lac de Thoune. *Mem. Soc. Physique et d'Hist. Nat. Genève*, T. 12, pp. 255-276, 1849.

- SRMONY, F.: Die Seen des Salzkammergutes. *Sitzber. d. math.-nat. Classe d. k. Akad. d. Wiss., Wien*, Bd. 4, s. 542-566, 1850.
- (34) *Journal*, Vol. 11, p. 4.
- (35) SANBORN, F. B.: Henry D. Thoreau. (American Men of Letters) *Boston and New York*, Houghton Mifflin Co., Revised Edition, 1910, pp. 244-245.
- (36) *Journal*, Vol. 18, p. 23.
- (37) *Ibid.*, Vol. 7, p. 464.
- (38) *Ibid.*, Vol. 12, p. 311.
- (39) *Ibid.*, Vol. 9, p. 156.
- (40) *Ibid.*, Vol. 20, p. 117.
- (41) MORE, P. E.: Thoreau's journal. In *Shelburne Essays*, Fifth Series, *Boston and New York*, Houghton Mifflin Co., 1910, pp. 106-131.
- CRAWFORD, B. V.: Henry David Thoreau. Representative Selections, with Introduction, Bibliography, and Notes (American Writers Series). *New York*, American Book Co., 1934.
- (42) *Journal*, Vol. 11, pp. 204-209.
- (43) *Ibid.*, Vol. 9, pp. 346-348.
- (44) *Ibid.*, Vol. 16, pp. 201, 269, 271-2.
- (45) CLEMENTS, F. E.: Plant succession. An analysis of the development of vegetation. *Carn. Inst. Wash.*, Pub. No. 242, 512 pp., 1916. Mr. J. W. Hechinger, however, states in a personal communication that he has found four references to American work in this field, published before 1850.
- (46) *Journal*, Vol. 20, pp. 232-239.
- (47) CANBY, H. S.: *Op. cit.*, p. 433.
- : The Works of Thoreau. *Boston*, Houghton Mifflin Co., 1937, p. 641.
- (48) CANBY, 1939, p. 324.
- (49) *Ibid.*, pp. 324-330.
- (50) MARCOU, J.: Life, Letters, and Works of Louis Agassiz. *New York and London*, Macmillan and Co., 2 vols., 1896.
- (51) CANBY, 1939, p. 431.
- (52) *Ibid.*, p. 324.
- (53) CANBY, 1937, pp. xv-xvi, 1939, pp. 334-336.
- (54) *Journal*, Vol. 13, p. 268.
- (55) *Ibid.*, Vol. 20, p. 323.
- (56) *Ibid.*, Vol. 16, p. 7.
- (57) *Ibid.*, p. 93.
- (58) *Walden*, pp. 315-316.





CONTROL OF SWIMMING POSITION BY MECHANICAL FACTORS AND PROPRIOCEPTION

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IT IS a well-known fact that most types of free-swimming Metazoa swim in characteristic positions. The body has usually a dorsal and a ventral surface, and the more typical animals swim with the back directed upwards. Some forms adopt the opposite position, with the back directed downwards, and there are various other orientations characteristic for certain species.

In many cases the normal position is maintained by an active reflex mechanism, which may be associated either with statocysts or with a response to light. Light, however, is often absent, and there are a large number of invertebrates in which statocysts have not been found. Proprioceptive orientation might occur, or orientation based on some special sensitivity to currents, but as yet we have no adequate evidence to support these possibilities.

It is particularly in the absence of any reflex orientation to stimuli that purely mechanical forces may be important for controlling the swimming position of an aquatic animal. In the present paper the discussion will center mainly on the various types of such mechanical orientation which theoretically might occur. The possible rôle of proprioception will be discussed briefly towards the end.

Although a large number of authors have appreciated that mechanical forces may be concerned in the swimming position of an aquatic animal, attempts to analyse these forces have not been satisfactory. There has been some valuable work on such topics as propulsive mechanisms and directional stability (see, for example, papers on fish by Magnan, 1929, 1930; and by Harris, 1936, 1937, 1938). But very little has been done on the mechanical factors which would favor return to a stable position. Perhaps the best papers in this

field are those of Bethe (1894, 1910) and Woltereck (1913). These, however, do not give a complete picture, and most later authors have underestimated the complexity of the problem, frequently reaching conclusions which were not justified by the experimental evidence available. There appears to be a real need for a simple statement of the nature of the problem, if for no other reason than to serve as a gentle caution. To supply this need it seems best to make the treatment as elementary as possible, perhaps to the disappointment of those who have any real appreciation of aero- or hydrodynamics.

POSSIBLE IMPORTANCE TO THE ANIMAL

At the outset it is perhaps appropriate to enquire what features of importance a stable position may possess for the swimming animal. One of the most obvious of these is to be seen when the specific gravity of the animal is greater than that of the water in which it lives. Such an animal will tend to sink, and this tendency must be resisted by some mechanism, for which it is important that the animal remain orientated with the correct side up. If the body becomes turned upside down the mechanism will act the wrong way, unless the animal is able to perceive its predicament and to reverse the mechanism.

Another important effect of a stable body position concerns the angle or direction of the swimming path in relation to the horizontal. If the body tends to lie in one particular position, any chance tip of the anterior end up or down will automatically be corrected, unless special steering organs are employed. The swimming path will thus remain at a more or less constant angle to the horizontal, with certain advantages to the animal which the ecologist will readily recognize (see, for example, Woltereck, 1913). From the normal

path the animal should be able to steer up or down at will, following some chosen direction with respect to the horizontal, without any need for a special sense to aid in orientation.

When the mechanically favored path is more vertical than horizontal the animal may appear to show positive or negative geotaxis. This fact has been recognized by former authors, and indeed mechanical control forms the basis of one of the theories advanced to account for geotaxis, as listed by Parker (1922) and by Dembowski (1929). It may be noted, however, that the theory has rarely if ever been found to supply the whole explanation for geotaxis in a given aquatic animal, although in the case of the ciliate, *Paramecium*, Dembowski (1931) has found that the theory will hold under certain special conditions.

In many animals the position of the body may affect not only the vertical inclination of the swimming path but also the directional stability for turns in the horizontal plane. This is particularly obvious in the case of animals which are laterally compressed. Typically there are certain vertical surfaces which offer a resistance to any tendency on the part of the animal to deviate to the left or right. If, however, the body tips over onto one side, these surfaces can no longer offer this resistance, and directional stability in the horizontal plane will probably be much reduced. The matter can be one of some importance to the animal because to wander in circles in a horizontal field may reduce the opportunities for finding fresh food, a mate, or other necessities in the environment.

For some animals it is possible that maintenance of the normal body position is of direct importance for health. If the animal were to lie too long in an abnormal position, there might be changes in internal organization, or some interference with organic function. Parr (1927) and Breder and Harris (1935-6) have claimed that this may actually be the case in certain fish.

For aquatic animals which live near the surface, or near the bottom, there may be yet other ways in which the maintenance of a stable swimming position can be significant, in connection with functions such as feeding and respiration. In some cases it is possible that animals swimming at intermediate depths may be able to catch sinking food particles better when lying in one position than when in another. Indeed for a majority of the free-swimming animals there are probably

several ways in which the swimming position is of importance, depending on the habits and environment of the species concerned.

It must be understood, however, that mechanical stability of position need not be wholly advantageous. If this were so we might expect that all swimming animals would be specially weighted along the lower surface. Such is not the case, probably largely because of the fact that too much stability reduces the ease with which the animal can manoeuvre. Some animals may be designed something like the modern transport aeroplane, with good stability, but without the capacity for turning rapidly in every direction. Others, more particularly those of more complex organization, will probably be much more like the fighting aeroplane, having the mechanical stability largely replaced by nervous control, and with well developed powers of turning rapidly in every sense required. In the case of fish it is known that many species rest in a position of slightly unstable equilibrium, maintaining the delicate balance by constant movements of their fins. It is tempting to suggest that the need for constant balancing has some survival value, serving to keep the fish alert, and ever ready for rapid movements in any direction.

BASIC TYPES OF MECHANICAL ORIENTATION

The forces which act upon the body of a swimming animal may be arranged in various ways. If the animal swims in some constant orientation relative to the axes of the earth, it is probable that this position will be one of equilibrium, in which all the forces balance. A chance rotation away from this orientation will disturb the balance, with the result that the body will either tend to rotate further, or will return to the original position. In the present section of this paper a discussion will be presented of the various arrangements of forces which might serve to control and maintain such a constant orientation. To simplify the problem the discussion will be illustrated by reference to simple geometrical bodies, rather than to the more complicated conditions which occur in actual animals.

The type of mechanism which first springs to mind is one in which the center of gravity tends to lie beneath a center of support. When the body is one with a specific gravity equal to that of the surrounding water, the support is wholly provided by the upward force of "buoyancy", acting through the center of buoyancy or center of mass of the displaced liquid, and equal in magnitude to the weight

of this liquid. If the body is of uniform density its centers of gravity and buoyancy will coincide, and it will float submerged in any position in a state of indifferent equilibrium. If, however, the body is not of uniform density the center of gravity will probably be displaced and the body will tend to float with this center vertically below the center of buoyancy (Fig. 1). Any chance rotation away from this position would establish a torque between the upward force of buoyancy and the downward pull of gravity, tending to restore the former position. Turned upside down the body would be in a position of unstable equilibrium, which could be maintained only by some system of careful balancing (as actually occurs in many kinds of fish).

The principle of the mechanism was clearly recognized by Borelli (1681), and it has since been well described by other biologists, such as Bethe

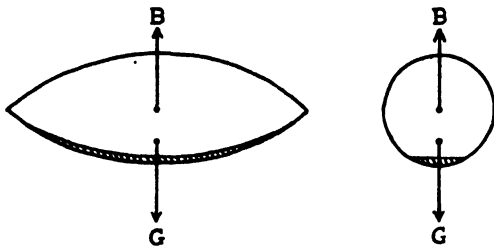


FIG. 1. LONGITUDINAL AND TRANSVERSE SECTIONS OF A BODY WITH TOTAL SPECIFIC GRAVITY EQUAL TO THAT OF THE SURROUNDING WATER

Shaded part denser than the rest. G and B represent the forces of gravity and buoyancy.

(1894, 1910), Müller (1919), and Magnan (1930). Yet the earlier paper by Bethe contains the statement that if a cone is thrown into a vacuum it will fall with the heavy end directed downwards. Although quite erroneous this statement has been quoted by some more recent authors (e. g. Magnus and de Kleijn, 1930), and it has perhaps led several other authors to express the view that the center of gravity will always tend to lie "as deep as possible", without giving any indication as to what point would tend to lie above it (Williams, 1900; Dembowski, 1929; Lowndes, 1937; in part also Alverdes, 1927; and Bethe, 1894, 1895). It must be pointed out that the force of gravity alone is not sufficient to produce orientation; in the simplest case there must be at least one other force, directed upwards, and not acting through the center of gravity except when the body is in a position of stable (or unstable) equilibrium.

The mechanism illustrated in Fig. 1 is of particular importance for bodies which have a specific gravity equal to that of the surrounding water. If opposing forces are absent such a mechanism will work almost equally well whether the body is stationary or moving, and it can also be effective when the body is of a specific gravity which is greater or less than that of the surrounding medium. In the latter cases, however, other forces usually become involved, and these may essentially alter the position of stable equilibrium.

Among free-swimming invertebrates there are many which have bodies with a specific gravity greater than that of the water in which they live. The force of buoyancy being thus insufficient to prevent sinking, the animals must provide some further support, either as a vertical component of the propulsive force, or as "dynamic lift" of the type which enables aeroplanes to fly.

It might be thought that under these conditions there would be a tendency for the center of gravity to lie underneath a new center of support, and indeed such a view has been expressed by some authors who have written on the flight of birds, of whom Borelli (1681) was probably the first. Plate (1924) advances the same view for animals which either fly or swim.

The requirements of this view would be met partially if we imagine an animal provided with appendages which within certain limits would automatically beat downwards, even if the body were tipped over to one side. This result might be achieved by having a certain degree of tension or elasticity in the basal parts of the appendages, allowing a graded amount of bending in response to the resistance of the water (Fig. 2). Under these conditions it would be possible to speak of an approximate center of support, lying between the two appendages, and of a tendency for the center of gravity to lie below this point. If, however, the body were turned more nearly upside down, the appendages could no longer beat downwards and the animal would probably sink helplessly, unless it was able to perceive the situation and to make the necessary reflex adjustments.

Among living animals it is doubtful if any examples can be found which possess a mechanism of the type just described. Certainly in the great majority of cases any upward force exerted by the animal is fixed in direction relative to the animal and not relative to the axes of the earth. If the animal tips over, away from the normal position,

the force will no longer act upwards to the same degree, unless the animal changes the mode of action of the propulsive organs. This means that it is no longer correct to speak of a tendency for the center of gravity to lie beneath a center of support. In fact the term "center of support", or "center of action of the supporting force", loses its meaning when the direction of this force is fixed relative to the body of the animal. A line of action for the force can be defined, but not a point of action,

animal should have a specific gravity which is not equal to that of the surrounding water.

Some of the general principles involved can be illustrated by reference to an imaginary spherical organism, heavier along one side than elsewhere, and propelled through the water by a propulsive force, P . To simplify the problem let it be supposed that the relative force of buoyancy is so small that it can be neglected. The body will then be acted upon by the downward force of gravity,

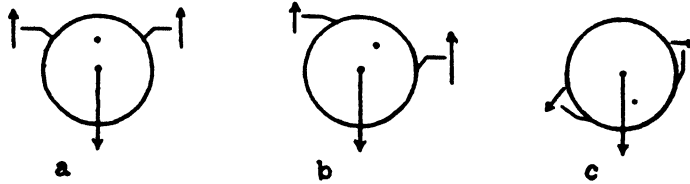


FIG. 2. TRANSVERSE SECTION OF IMAGINARY ANIMAL PROVIDED WITH APPENDAGES WHICH PRODUCE A FORCE AUTOMATICALLY DIRECTED UPWARDS (a, b), EXCEPT WHEN THE BODY HAS ROTATED OVER TOO FAR (c)

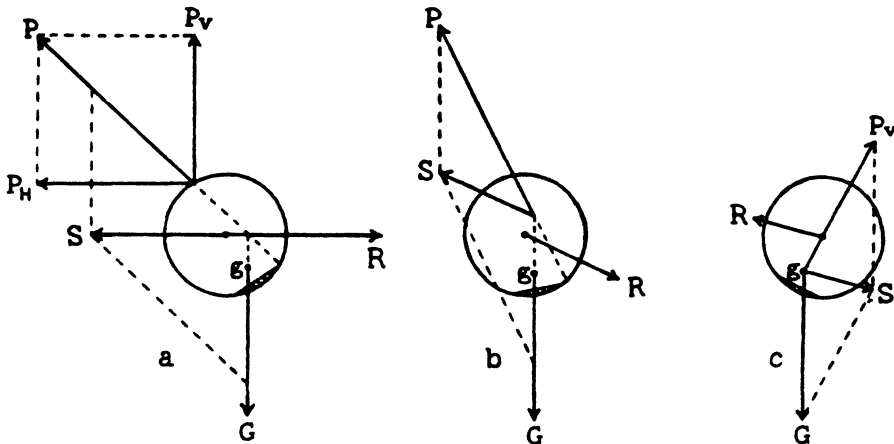


FIG. 3. HYPOTHETICAL SPHERICAL ORGANISM. (a) ANTERO-POSTERIOR SECTION, STABLE EQUILIBRIUM POSITION. (b) DITTO, UNSTABLE POSITION AFTER ROTATION AROUND TRANSVERSE AXIS. (c) TRANSVERSE SECTION, UNSTABLE POSITION AFTER ROTATION AROUND ANTERO-POSTERIOR AXIS

P = propulsive force (P_v and P_h the vertical and horizontal components), G = force of gravity, S = resultant of these two forces. R = resistance. g = center of gravity.

since there is no one point along the line through which the force can be said to act more than it does through any other.

Mechanical control of the orientation of a swimming animal might, however, be achieved in a number of other ways, which do not depend on the presence of a fixed center of support. The mechanisms here concerned are all somewhat complex, involving the interrelationships between at least three forces, those of gravity, propulsion, and resistance. In each case it is essential that the

G , and it will be subjected to a net pull, S , representing the resultant of the forces G and P . Let the magnitude and direction of the force P be as shown in Fig. 3a, such that when the resultant force S acts along a line which is horizontal, this line will pass through the center of the sphere. P_v , the vertical component of the propulsive force, would then be equal to G , and the body would be pulled forward horizontally by the force P_h , here equal to S . Opposed to the forward motion there would be a resistance, R , acting through the center

of the sphere, and also through the point of intersection of the forces G and P.

It will be seen that under these conditions the position of the body is one of equilibrium, in which all the forces balance. Any slight rotation around an axis at right angles to the paper would cause a shift in the line of action of the resultant force S, such that a couple would be created between the forces S and R (Fig. 3b). Inspection shows that the rotational force of this couple would always act in a direction tending to restore the former position of equilibrium, which consequently represents a stable orientation. Fig. 3c shows that the equilibrium position would also be restored after any rotations around an "antero-posterior" axis, which in Fig. 3a would lie in the plane of the paper.

Neglect of the upward force of buoyancy would not be justified if the body were really that of a free-swimming animal, since no such animals have specific gravities much above that of the surrounding water. The equilibrium position for the body represented in Fig. 3 becomes somewhat modified if the effects of buoyancy are considered in addition to those of the other forces. A torque between the forces of buoyancy and gravity would tend to bring the center of gravity more nearly below the center of the sphere. This, however, would set up a counteracting couple between the forces S and R, so that equilibrium would be reached when the position was such that the opposing rotational forces just balanced. In this new equilibrium position the resultant of the three forces of buoyancy, propulsion, and gravity, would be equal and opposite to the resistance and would follow the same line of action. Some alteration of the magnitude or direction of the force P would be necessary, if it was desired that the body should continue to progress forward horizontally.

The line of action of the fluid resistance is particularly easy to predict in the case of a sphere, the shape of which is such that the resistance always acts through the center of the body, following a line parallel to the direction of motion. For bodies of other shapes the problem becomes more complicated, because there can be no one point through which the resistance will always act, nor will the line of action of this force necessarily be parallel to the direction of movement. The complications introduced by these facts are difficult to analyze in simple geometrical drawings, but a few general points must be discussed here, since not many animals are even approximately spherical.

At the outset it seems advisable to describe more precisely what is meant by the term "fluid resistance." It is well known that when a body moves through water it meets with a kind of dynamic pressure or resistance which opposes the motion. To some extent such resistance is caused by surface friction. Usually to a much greater extent it is caused by resistance of the water to displacement, and comparison might be made with the situation which would occur if the body were pushed through an easily deformable solid. Resistance in this latter case would depend on both the amount and the rate of the displacement. A tapering, pointed object displaces the surrounding solid more gradually than does one in which the end is blunt, and so it meets with less resistance. In the case of a fluid, however, the situation is profoundly modified by the way in which the fluid closes in behind a moving body. Pressures or resistances thus act behind the body and along its sides as well as directly in front. The consequences of this phenomenon will be easily appreciated if reference is made to the subject of "stream-line form." The important point to recognize is that dynamic fluid pressure acts on all parts of the body, changing in its magnitude and direction from one region to another. In general the fluid exerts the greatest pressure where its rate of flow is least, as has been expressed in Bernoulli's theorem.

A moving body will tend to adopt a position in which the fluid pressures balance around an axis representing the resultant of the other forces applied to the body. This resultant shifts its position with every change in the orientation of the body relative to the axes of the earth, and the problem can be especially complicated when the resultant does not always pass through the center of gravity (as, for example, in Fig. 3). A simpler case is afforded by a body of uniform density sinking passively under the influence of gravity alone. Under such conditions the body would tend to assume a position in which all the forces balanced around a vertical line drawn through the center of gravity. In some cases there might be several such balance or equilibrium positions, but for bodies of some shapes only one of these positions would represent a really stable orientation.

If an attempt is made to predict what this orientation would be for a body of given shape, there is one important general theorem which can be of service, to which the attention of biologists

has been directed by Lowndes (1937). The theorem states that if a body is moving freely through a fluid, under the influence of external forces, it will tend to adopt a position in which a maximum cross-sectional area is placed across the direction of motion. The factors concerned in a simple case are given full mathematical treatment, as well as an explanatory diagram, in Lamb (1924, pp. 82 and 154-6).

But frequently there may be at least two quite different orientations which satisfy the requirements of the theorem, as for instance in the case of an elongated animal with dorso-ventral differentiation. Probably in most cases there would be a tendency to assume one of these orientations more

along the longer axis. When the body lies with the pole, p , directed upwards it will neither sink nor rise (Fig. 4a). If it tips over to one side it will become subjected to the resultant force, S , which will pull it sideways and somewhat downwards. The resistance which is met with will be such as to tend to set the body broadside on to the direction of motion, or in other words there will be a couple tending to restore the former position. The same would be true for any further degree of rotation, as may be seen from Figs. 4b and 4c. The position shown in Fig. 4a is thus one of stable equilibrium.

If the force, P , is pulling forwards as well as upwards quite a different situation will exist with regard to the rotations around the "transverse"

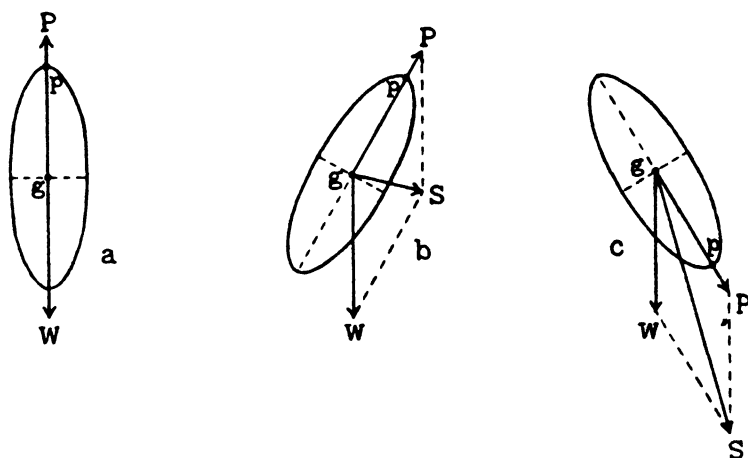


FIG. 4. TRANSVERSE SECTION OF ANIMAL WHICH RESISTS THE TENDENCY TO SINK BY AN UPWARD PROPULSIVE FORCE. (a) STABLE POSITION. (b, c) UNSTABLE POSITIONS

W = force due to weight of the body in water (equal to the force of gravity less that of buoyancy). p = dorsal pole. Other letters as in Fig. 3.

often than the other, and perhaps the favored position would usually be the one offering the least resistance. How far that would be found to represent a general rule seems rather doubtful, but Bethe (1894) probably had such an idea in mind when he claimed that a sinking body will occupy the position which offers the least resistance. His statement is not in agreement with the theorem quoted above, but perhaps it was intended to apply only to the choice of positions which may exist after the requirements of that theorem have been already met.

Turning to consider some concrete examples, we may begin by considering the case of a body which is oval in cross-section, and in which the tendency to sink is resisted by an upward force, P , acting

axis. It can be supposed, for example, that the body seen in transverse section in Fig. 4, is cigar-shaped when seen in longitudinal section. The force, P , can be placed so as to act diagonally through the center of gravity, such that when the longitudinal axis of the body is horizontal the vertical component, P_v , then exactly balances the downward force, W (Fig. 5a). Under such conditions the body would be in equilibrium and would move forward horizontally. A tilt of the nose up or down, however, would cause the resultant of the forces, P and W , to move above the longitudinal axis. The body would now tend to set itself broadside on to the direction of pull, and thus it would rotate in the direction indicated by the curved arrows (Figs. 5b and 5c). It will be seen

that the direction of rotation is the same in each case, and in fact the body would rotate continuously once it had left the position of unstable equilibrium represented in Fig. 5a. The same would be true for a body of greater height than length, except that the rotations would be in the opposite direction.

Various other possibilities emerge when we consider bodies which are not symmetrical above and below a median horizontal plane. For example the addition of a pair of sloping wings can reverse the stability of a body which is oval in cross-section,

down, but the range of rotations over which there would be any tendency for return to this position would be relatively small (Fig. 6c).

Yet another situation is created if the body is supported by a vertical component of the resistance, the so-called "dynamic lift", instead of by a vertical component of the propulsive force. Under these conditions the propulsive force can be arranged to act directly forwards, and at a certain speed of forward movement the upward lift will exactly balance the forces pulling downward. The factors which control stability of orientation are

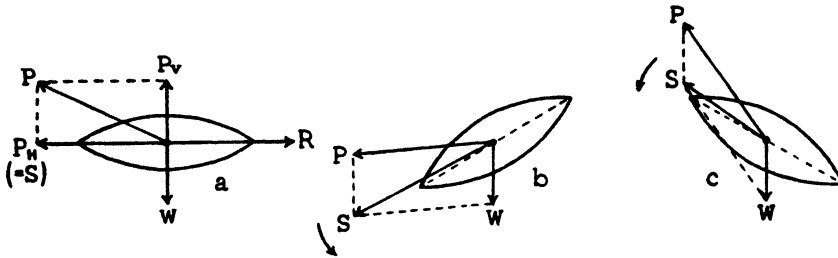


FIG. 5. CIGAR-SHAPED BODY PROPELLED BY A FORCE ACTING DIAGONALLY THROUGH THE CENTER OF GRAVITY. (a) POSITION OF UNSTABLE EQUILIBRIUM. (b, c) UNSTABLE POSITIONS WITH NO EQUILIBRIUM

Lettering as in Figs. 3 and 4

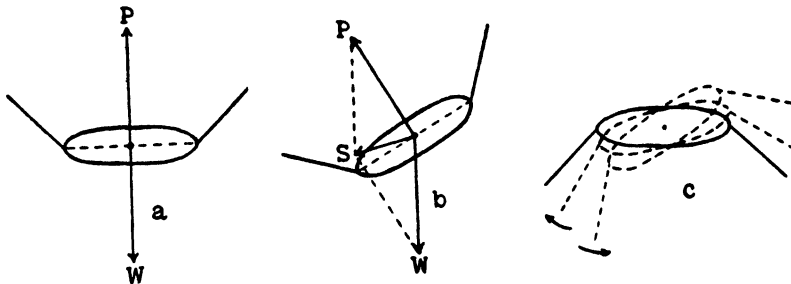


FIG. 6. TRANSVERSE SECTION OF A BODY WITH FIXED SLOPING WINGS, WHICH RESISTS THE TENDENCY TO SINK BY AN UPWARD PROPULSIVE FORCE. (a) STABLE POSITION. (b) UNSTABLE POSITION. (c) POSITION OF LIMITED STABILITY—INDICATED BY BROKEN LINES ARE TWO UNSTABLE POSITIONS, FROM WHICH THE BODY WOULD TEND TO RETURN TOWARDS 'c' AND TOWARDS 'a' RESPECTIVELY.

tion, and which exerts a force, P , acting along the shorter axis (Fig. 6). Without the wings such a body would not remain in stable equilibrium when the force, P , was directed upwards, but rather it would tend to turn over and sink. With sloping wings attached as shown, the position in which the force, P , is directed upwards becomes one of stable equilibrium, to which the body would tend to return after all except the most extreme degrees of rotation around its longitudinal axis. A more precarious position of stable equilibrium would also exist when the body was turned completely upside

then somewhat different from those which have been described in the examples given above. They can perhaps be illustrated best by reference to the part which they play in controlling the stability of an aeroplane. (A good popular account of stability in aeroplanes is given by v. Mises (1936).)

The orientation of an aeroplane can be disturbed by rotations either around the longitudinal axis or around the transverse axis, and these two types of rotation must be considered separately. For the rotations around the longitudinal axis there are some aeroplanes which are relatively stable, but

there are others which are not. The latter type are constructed with wings which extend out horizontally from the body, so that the wings of opposite sides lie in the same geometrical plane. If an aeroplane of this type tips over to one side while it is flying straight forward at constant speed, the lifting force, L , will continue to act at right angles to the wings and will remain unchanged in magnitude. The aeroplane will thus be subjected to a sideways and downward pull, representing the resultant between the forces L and W (Fig. 7). The resistance which is met will tend to set the aeroplane broadside on to the direction of pull, and since the pull passes above the wing the aeroplane will tend to turn over. The normal flying position is thus one of unstable

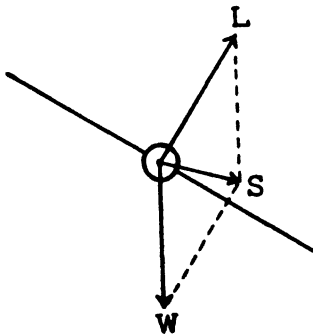


FIG. 7. TRANSVERSE SECTION OF AEROPLANE WITH PARALLEL WINGS FLYING IN AN UNSTABLE POSITION, IN WHICH THE TENDENCY WOULD BE TO TURN UPSIDE DOWN.

L = force of "dynamic lift." W = downward pull due to the weight. S = resultant of these two forces.

equilibrium, which can be maintained only by constant vigilance on the part of the pilot.

It is hardly surprising that in most aeroplanes some attempt is made to change this state of affairs. The method used consists in attaching the wings so that they slope slightly upwards from the body, out towards their free ends. A very small degree of slope is sufficient to ensure considerable stability. If the aeroplane tips over during flight it will start to slip sideways and downwards as described above. Air now meets the lower of the two wings at a greater "angle of attack" than it does the upper wing, and the result of this is a difference in the lift exerted on the two sides, tending to restore the aeroplane to its former position. It may be noted in this connection that the wings usually slope somewhat upwards from

back to front (so as to offer a small "positive" angle of attack), and that consequently during forward movement the air usually strikes the lower surface first, even when the aeroplane is slipping sideways under the influence of a pull acting along a line above the wing. It is also of some importance that the shape of the wings, as seen in cross-section, is such that they continue to supply some upward lift even when the angle of attack is slightly "negative."

Another method to ensure stability for rotations around the longitudinal axis would be to provide the aeroplane with enormous median vertical fins, so as to give the sagittal plane a greater area than that which is offered by the wings. There would now be no need for the two wings to slope upwards towards their free ends, since the conditions would be essentially similar to those shown in Fig. 4. The arrangement would not be practicable for normal aeroplanes, but in many aquatic animals a corresponding arrangement may well be found. As has been noted before, the specific gravity of aquatic animals is never much above that of the water in which they live, so that only a small lifting force is required. This force could be supplied by a very small pair of wings, or indeed without any wings at all if the shape of the body and its "angle of attack" were such that pressure on the lower surface exceeded that above. Under these conditions the depth of the body easily might be greater than the width, in which case the type of stability illustrated in Fig. 4 might be present.

Turning now to consider the control of rotations around the transverse axis, it can be shown that in the aeroplane this is largely due to the action of the horizontal tail fin. When flying forward horizontally the aeroplane is subject to a net pull, S , which represents the resultant of the two forces, P and W . This pull is exactly balanced by the resistance, R , and if the aeroplane is correctly "trimmed" the tail fin will be exactly horizontal and therefore not contributing to the lift. If an aeroplane which is trimmed in this way should attempt to fly diagonally downwards or upwards, the direction of the force S will be changed relative to the machine. As a result of this the aeroplane would take up a slightly different angle of attack, thus exposing the tail fin to extra pressure, above or below as the case may be (Fig. 8). It will be seen that these new pressures on the tail are such

as to cause the aeroplane to return to a horizontal course.

Pressures of the same kind are especially well developed during and immediately after any chance departures from a horizontal path. For a few moments the force of inertia causes the machine still to follow that path, although the body is pointed in a new direction. The horizontal tail fin is consequently exposed to a considerable pressure, which tends to restore the machine to its former orientation. If, however, the return to this position is in some way delayed, the aeroplane will start to fly in the new direction, and very soon the pressure on the tail will disappear except for a certain amount which can be attributed to the factors discussed in the last paragraph. The purely momentary pressure which arises during

active jumps. If the jumps are directed diagonally upward and the pauses are of a suitable length, the net forward path will be horizontal. A considerable number of aquatic animals exhibit this type of swimming, and an excellent analysis of some of the factors concerned in the case of Cladocera has been given by Woltereck (1913).

It is of interest to note that Bethe (1910) held the opinion that the shape of a swimming animal can be of importance for controlling its orientation only if the progression is discontinuous. Lowndes (1937) has rightly stressed the more general importance of body shape, but he appears to overlook the fact that orientation cannot be controlled by this factor except when the specific gravity of the body is definitely above that of the surrounding water.

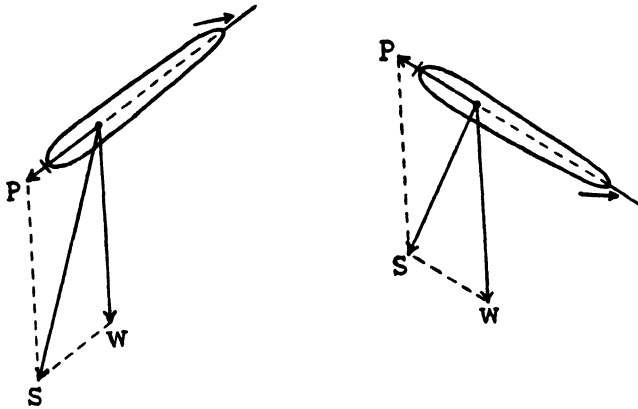


FIG. 8. LONGITUDINAL SECTIONS OF AEROPLANE TRIMMED FOR HORIZONTAL FLIGHT, SHOWN AS ATTEMPTING TO FLY DIAGONALLY DOWNWARDS AND UPWARDS

and after a change of orientation is of great importance for directional stability, but it cannot serve to maintain a body in some constant orientation relative to the axes of the earth.

A comparison of the conditions illustrated in Fig. 8, with those shown in Fig. 5, suggests that stability in regard to rotations around the transverse axis can more easily be attained when support is provided by "dynamic lift," than when it is provided by a vertical component of the propulsive force. In cases of the latter kind, however, the difficulties can be overcome if forward progression occurs as a series of jumps, each one followed by a pause during which the body has time to reach approximately the position seen during passive sinking. An arrangement of this type allows the body to be constantly re-orientated, no matter to what extent the orientation may be lost during the

If an attempt is made to summarize the various ways in which the orientation of swimming animals might be mechanically controlled, it appears that there are perhaps three basic mechanisms which are more likely to occur than any others. The first of these is the mechanism involving a relationship between the centers of gravity and buoyancy. This is the only mechanism possible in animals which have a specific gravity equal to that of the surrounding water. It may also be important in animals with a specific gravity exceeding that of the water, but there are then various other mechanisms possible, of which two seem especially likely to occur. If the animal is one in which the tendency to sink is resisted by a vertical component of the propulsive force, it will probably swim in jumps, allowing its body to be orientated by fluid pressures during the brief periods of passive sink-

ing. If the supporting force is provided by "dynamic lift" the animal will perhaps swim continuously and its orientation may be controlled by some mechanism similar to that which exists in the aeroplane.

When efforts are made to apply such theoretical conclusions to actual living animals the difficulties may increase enormously. Reasons for this are, first, the changes in shape so often seen when the animal swims; and, second, the complex system of currents which the animal may create by its own activity. Changes in shape during swimming may essentially alter the effective shape of the animal and its relation to the surrounding fluid pressure. This is a factor difficult to estimate or to test experimentally, but it must be considered when trying to interpret results obtained with non-living material. Even more important may be the effects of currents created by the animal. It was noted above that fluid pressure and the rate of fluid flow are closely related, so that it will readily be understood that a complex system of currents around a swimming animal may greatly alter the pattern of fluid pressure which is met with during movement. In a sense it may be said that the effective shape of the animal has been altered. The currents which are created by the animal's own activity can be thought of as forming a permanent shell or envelope around the body. If the animal starts to sink it is this envelope which meets the water lying ahead, and which determines its lines of flow on being displaced.

SOME EXPERIMENTAL METHODS

An experimental analysis of mechanical factors concerned with orientation in a given animal may sometimes be extremely difficult. Not only may there be complications of the type just described, but the various mechanisms which are possible may be modified or combined together in almost any way. Some of the more complex cases are probably beyond the scope of experimental methods known at present. Nevertheless it should be of some value to review briefly such methods as have been used by previous investigators, or which might be tried in the near future.

To find the position of the center of gravity the simplest method is that used by Magnan (1929). Working with various species of fish he first found the position in which the body would balance horizontally when laid across a sharp edge. He then suspended the animal from one end or from one of the fins. Vertical lines from the points of

balance and of suspension were drawn in each case, and the point in the median plane at which these lines crossed was taken to represent the center of gravity. Fish with flexible bodies were laid across the two pans of a balance and the position adjusted until the median pointer remained vertical.

For small invertebrates the problem is more difficult. Müller (1919) describes a method which he used to determine the horizontal balance position in a fairy shrimp (Crustacea Anostraca). He did not, however, attempt to define the position of the center of gravity more precisely.

In all such experiments certain precautions are necessary. The animal should be killed or narcotized in a manner which does not cause local changes in specific gravity. The shape of the body and the contents of the gut must be normal. If the determinations are made in air the surface of the body should be carefully dried, yet at the same time there must be no loss of internal fluids. Some of these difficulties might be avoided if the determinations could be carried out under water. This, however, would not be possible except for animals with a specific gravity considerably above that of the water, and it would require special care to avoid the disturbing action of local currents.

The position of the center of buoyancy can be found by constructing a model of uniform density and then finding the center of gravity of this model. Magnan (1929) employed this method for fish. He also used a method which did not give the exact position of the center of buoyancy, but which showed how far it was in front of or behind the center of gravity. For this purpose a fish was supported under water by a pin which pierced the body transversely through the center of gravity. Small weights were then placed on the back, near this region, and shifted until the long axis of the body came to lie just horizontal. A simple calculation gave the required result.

For small and soft-bodied animals accurate determinations of the positions of the centers of gravity and buoyancy become almost impossible. Usually the best that can be done is to determine the relative positions of these two centers to each other. To do this it is necessary to float the body of the animal in a liquid of a specific gravity equal to its own. If the two centers coincide the body will be in indifferent equilibrium and will float in any position. If the two centers do not coincide there will be a tendency for the center of gravity to lie vertically below the center of buoyancy. Some idea of the distance apart of the two centers

will be indicated by the speed of rotation towards this position of stable equilibrium.

The method was employed by Müller (1919), but it is one which requires a number of precautions which he did not clearly state. To avoid possible local changes in specific gravity the animals should be lightly narcotized, or perhaps killed by a mild electric shock. Attention should be paid to the shape of the body, contents of the gut, and such factors as the number of eggs or young. (The effects of gut contents and of young on the specific gravity of Cladocera have been described by Eyden (1923) and by Luntz (1929).) If it is necessary to raise the specific gravity of the water, the solute chosen for this purpose should preferably be non-toxic, have a low osmotic pressure, and a low rate of penetration through the skin of the animal. A high viscosity should also be avoided. During observations of specimens placed in this solution care should be taken to see that the specific gravity of the solution is correct, that it is evenly mixed, and that there are no disturbing currents. The specimens should be free from any liquid of a different density enclosed between limbs or clinging to other parts of the body. All the observations should be carried out as rapidly as possible so that interchanges between the body fluids and the solution may be reduced to a minimum.

The extent to which the forces of buoyancy and gravity may control orientation during swimming can be studied directly, if it is possible to allow the animal to swim in a solution of the type just described. The absence of any tendency to sink eliminates the possible influence of other methods of mechanical control, and most types of sensory mechanism can usually be excluded by suitable design of the experiment. Mechanical control by the forces of buoyancy and gravity, and perhaps some form of proprioception, then remain as the only possible explanations of any orientation which may occur. Good evidence in favor of the mechanical control would be secured if the animal swam in a position similar to that in which narcotized specimens had been found to float. Orientation by proprioception might still occur, but as will be shown later this remains at present as a rather doubtful possibility.

For animals whose specific gravity is equal to that of the water in which they live the only type of mechanical orientation possible is that which depends on the relative positions of the centers of gravity and buoyancy. In practice, however, it

seems that a large number of free-swimming animals have a specific gravity somewhat above that of the water and that they persistently oppose the tendency to sink. Under these conditions other mechanisms can play their part and must, therefore, be considered in any study of mechanical orientation in the animals concerned.

To show whether or not the specific gravity is above that of the water, it is sufficient simply to watch an animal which has ceased to swim. To obtain a more quantitative value of the specific gravity a number of methods may be employed. That which has been used most frequently is based on the same floatation technique as has been just described. It is only necessary to know the specific gravity of the solution in which narcotized specimens of the animal will float without rising or sinking. The results obtained are usually not very accurate, although this may sometimes be due to neglect of the precautions listed above. Platt, however, (1899) gives figures for *Spirosomum* which appear to indicate an accuracy of about ± 0.001 , and Luntz (1929) gives figures for rotifers which seem accurate to about ± 0.004 . Ostwald (1903) has pointed out that the results will be least accurate when the viscosity of the medium and the surface resistance offered by the animal are unduly large. He suggests a modification of the method, by which he believes greater accuracy would be obtained. Instead of attempting to mix a solution in which the body will exactly float, he would prepare two solutions, in one of which the body would slowly rise, in the other of which it would slowly sink. The speeds of rising and sinking could be determined, and the specific gravity of the body would then be given by the

formula, $S_k = \frac{G_1 S_2 - G_2 S_1}{G_1 - G_2}$, where S_k , S_1 and S_2

are the specific gravities of the body and of the two solutions, and where G_1 and G_2 are the speeds of sinking and rising which were observed. Ostwald assumes that in liquids of specific gravities equidistant above and below S_k , the rates of rise and fall would be equal. He states that this would actually be true, unless certain movable parts were extended during the motion in one direction, but were folded up during motion in the other. On this question, however, Ostwald has missed the essential point, namely that orientation of the body relative to the direction of motion must be made the same in each case. If this condition is not observed the fluid pressures met with during

rising and sinking will be different, except in the case of a body of identical form above and below. In practice this means that in all cases in which the centers of gravity and buoyancy do not coincide, the speeds of rise and fall must be fairly rapid, so as to ensure an orientation controlled entirely in the manner which has been illustrated in Fig. 6. This increases the difficulty, which was pointed out by Ostwald, of being certain as to whether or not a steady rate of motion has been attained.

Lowndes (1938a, b) has recently described a new method for determining specific gravity, which is apparently free from many of the objections associated with the previous methods. Titration of some substance added to the water affords a neat means of determining the actual volume of the animals, and the weight can then be found by a simple calculation involving this result and the results of weighing in specific gravity bottles. In a control test with small glass bubbles Lowndes found the results were accurate to about ± 0.002 .

For large animals, such as fish, the weight can be determined in air, and the volume ascertained by direct measurement of the water displacement (Magnan, 1929). Or the weight may be determined both in air and in water, and the specific gravity then calculated from the formula,
$$S.G. = \frac{W_a}{W_a - W_w}$$
 where W_a and W_w represent the weights in air and water respectively (Tester, 1940). For small, spherical organisms, some use might be made of the well known method involving Stoke's law. Literature for various methods which have been used to determine the specific gravity of Protozoa is cited by Leontjew (1928).

From the point of view of animal orientation a determination of the specific gravity is not of fundamental importance, although it does permit a quantitative estimate to be made of the force which is required to prevent sinking. More important in this connection is a knowledge of the lines of action of the forces of propulsion and resistance. Unfortunately the methods which might be used to obtain this knowledge are not very satisfactory.

To determine the line of action of the propulsive force there seems to be little that can be done, other than to study the mode of action of the propulsive organs and the distribution of the currents which they create. Data secured in this way would indicate approximately the line of action

of the propulsive force, but would not define its location with any great degree of accuracy.

Methods for observing the currents which surround a swimming animal usually depend on the addition of a suitable dye or of small particles to the water. The path and speed of such particles can be determined by appropriate methods of photography. An interesting technique which can be used to study some of the more definite currents, consists in adding to the water particles of tobacco mosaic virus, the observations being carried out through crossed polaroid plates which are placed on opposite sides of the vessel. The tiny, rod-shaped particles of the virus become orientated parallel to one another wherever there is a current, and they then possess the property of rotating plane polarised light, thus causing the currents to appear as bright streaks in an otherwise darker field (cf. Bawden *et al.*, 1936).

To determine the lines of action of the fluid resistance which is met with by a swimming animal is no less difficult than in the case of the propulsive force. Such methods of investigation as exist can mostly be applied only to dead or narcotized animals, and the results obtained may consequently have little direct application to the animals when alive.

It is relatively simple to determine the effects of fluid resistance on the orientation of the body when this is sinking passively in water. If the centers of gravity and buoyancy are known to coincide no experiment would be necessary, other than to observe the position in which the body sinks. If, however, the position which is then observed is one which might be caused by the tendency of the center of gravity to lie below the center of buoyancy, further tests have to be carried out. In a particular example let us suppose that during passive sinking the same position is favored both by the fluid resistance and by the forces of gravity and buoyancy. This state of affairs could be demonstrated by transferring the narcotized specimen to fluids of greater density, adopting the precautions which have been outlined above. In a liquid in which the body very slowly rises, the orientation would remain the same as that seen during sinking. But in liquids of still higher density the rate of rising would increase, until finally the specimen would turn over because the effect of the fluid resistance had overcome that of the forces of buoyancy and gravity.

The essential features of this experiment were

It seems quite possible that proprioception of the second type may sometimes serve to control the orientation of certain fish. Rizzolo (1929) has shown that dogfish continue to swim in the normal position after total destruction of both the labyrinths, accompanied by transection of the olfactory tracts and of the optic nerves. The data given by Magnan (1929) indicate that these fish have a specific gravity only very slightly higher than that of sea water, and that they have the center of gravity placed a little above the center of buoyancy. These facts make it unlikely that the swimming position can be controlled by purely mechanical factors. Sensory control would thus appear to be involved, but the precise nature of this remains uncertain. It might be based on proprioception, or on a skin sensitivity to light, or on the perception of currents reflected from the sides and bottom of the aquarium.

V. Buddenbrock (1914, 1937) claims that proprioceptive orientation may be shown to exist in certain aquatic invertebrates. He suggests that this orientation occurs in response to movements of internal organs suspended in the body cavity. Experimental support for this idea was advanced by Wolf (1925), who found that in starfish a stimulus for orientation is provided by passive movements of the gut. Fraenkel (1928), however, claims to have disproved Wolf's results, and it would appear that proprioception of this type has not been proved to exist in any invertebrates. In particular nothing is known of the types of proprioception which perhaps occur in the species which are free-swimming.

Evidence that some type of proprioceptive orientation does occur in these forms is brought forward by v. Buddenbrock (1914). Most of his results, however, could be explained almost equally well on a purely mechanical basis. In one type of experiment v. Buddenbrock found that if the two crustaceans, *Leptomysis* and *Hemimysis*, were deprived of their statocysts and then placed in a horizontal beam of light, they swam vertically up and down, with their backs directed towards the light. The animals never swam horizontally, although their backs could have been turned towards the light in this position also. It was claimed that this result showed the existence of a proprioceptive sense of orientation. Another explanation, however, might be suggested. In order to swim horizontally with their backs towards the light the animals would have been compelled to lie

on one side, a position which in many animals is mechanically more unstable than any other. The apparent choice of a vertical path may thus have been due to the fact that the animals were not able to orientate effectively to the light when they attempted to swim horizontally.

In another experiment v. Buddenbrock found that if *Hemimysis* was kept in bright sunlight and then suddenly transferred into red light, the animals continued to swim in the normal position, although both the statocysts had been removed. It was assumed that the light-adapted animals were not able to perceive the red light and that the position in which they swam was mechanically unstable. These assumptions, however, were not supported by experimental evidence. With *Palaemon* v. Buddenbrock found that adult individuals from which the statocysts had been removed would often persistently swim with the back directed upwards, even when illuminated only from below. The position adopted was again supposed to be mechanically unstable, but no attempt was made to offer experimental proof.

Perhaps the most convincing experiments which favor the idea of proprioceptive orientation in a free-swimming form, were those of Demoll (1909) on the crustacean, *Squilla*. Demoll found that blinded individuals of this animal persistently swam with the back directed upwards, even when the back was weighted by small pieces of lead which were over one fifth the total weight of the body. It was especially noted that the animals soon turned upside down whenever the swimming movements became less energetic. This makes it clear that a tendency for the center of gravity to lie below the center of buoyancy could not have been responsible for the animal's continued ability to maintain the normal position. Some other mechanism might have been concerned, in which the magnitude of the force of propulsion or resistance played an essential part (for example a mechanism such as that illustrated in Fig. 4), but this appears most unlikely. Demoll assumed that the blinded animals would not be able to orientate to light, and in this he probably was correct. Nevertheless dorso-ventral orientation to light may sometimes be controlled by photosensitivity of the skin, as for example in the leech (Schlüter, 1933) and perhaps in certain beetle larvae (Wojtusiak, 1929). This might also be true for *Squilla*, though v. Buddenbrock (1914) found that unblinded adult animals did not always turn upside down when

the light was placed below, so that the reflex orientation to light is not especially well developed. The possibility remains that the orientation is controlled by statocysts, as was supposed by Demoll. But no such organs have yet been found in *Squilla*, and v. Buddenbrock argues on physiological grounds that they probably do not occur.

Recently the view that proprioceptive orientation may occur in free-swimming animals has been supported by Oevermann (1936), who worked with aquatic Hemiptera. He claimed that when these animals are in need of air they still are able to find the water surface, even after being blinded and deprived of their antennae, after having the abdominal nerve cord cut through, and with the body weighted so that the usual swimming position has become unstable. He also maintained that the animals will attempt to preserve the normal swimming position, even when this has been rendered unstable by the attachment of weights or by the removal of air from the surface of the body. These experiments are of great interest, but unfortunately Oevermann's descriptions are not always sufficiently objective, and no experimental evidence was given concerning the alleged stability or otherwise of the different swimming positions which he observed.

If proprioceptive orientation should be shown to be absent in a free-swimming animal, this would not necessarily mean the absence of proprioception. Bethe (1894) denied that a purely proprioceptive orientation could occur in swimming or flying animals. Yet he maintained that if mechanical forces favored one position the animal would always know the angle at which it lay in relation to this position, simply by the feeling in the muscles. It is possible that Bethe believed that the amount of mechanical torque within the body could be perceived directly, although this seems most unlikely. More probable would be some form of proprioception within such various steering organs as are required to deflect the animal from the stable orientation.

Sensory control of the swimming position might also be based on a surface sensitivity to currents. In animals with a specific gravity above that of the surrounding water there would be a tendency to sink whenever the normal swimming position is temporarily lost. At such times the pattern of currents around the body would be changed, and if the animal could perceive these changes reflex righting movements might occur. Alverdes (1927)

has suggested a sensory mechanism of somewhat this type for larvae of the insect *Clæon*.

Close to the bottom or to the surface of the water some reflex orientation might occur through the perception of "echo currents." Townsend (1939) has reported a sensory perception of this kind in the heteronereis stage of a species of polychaete worm, and a similar function can be ascribed to the lateral line organs of certain fish (Dykgraaf, 1934).

DISCUSSION

The orientation of a typical free-swimming animal involves rotations around three major axes, longitudinal, dorso-ventral, and transverse. There are, however, two main types of orientation, of which that discussed in the present paper can be described as "dorso-ventral" and involves rotations around only the transverse and longitudinal axes. Control of these rotations may be purely mechanical or it may be reflex and sensory. The situation is complicated because several types of control may act together, or there may be various factors which are opposed to each other. Investigations of dorso-ventral orientation must therefore deal with all these different factors, and an experiment which takes into account only the sensory or only the mechanical factors, may easily lead to a false result.

The second of the two main types of orientation is that which is involved in the familiar "phototaxis" and in various other forms of "taxis." Orientation of this kind may be described as "antero-posterior" and is associated with rotations around the transverse and dorso-ventral axes. The control of rotations around the latter axis must be always sensory, unless the animal lies on one side, but control of the rotations around the transverse axis may be either sensory or mechanical. This means in practice that, if an experiment on any form of taxis is concerned with turns up or down, then mechanical as well as sensory factors must be given full consideration.

Mechanical factors very similar to those involved in orientation are also of great importance in the problems connected with floatation (reviewed by Jacobs, 1935) and with cyclomorphosis (reviewed for *Daphnia* by Coker, 1939). The earlier workers in these fields were often inclined to exaggerate some one particular feature, while they overlooked the important relations which may exist between the shape of the body and the

pattern of surrounding fluid pressure. Thus Wesenberg-Lund (1908) was of the opinion that the spines and other outgrowths of planktonic organisms are of special importance because they shift the position of the center of gravity. It was the brilliant work of Woltereck (1913) which first clearly showed that such organs may play a significant rôle in controlling the orientation of the body relative to its line of motion, by virtue of the resistance which they offer to movement through the water.

SUMMARY

1. Most aquatic animals swim in some typical position which bears a definite relation to the axes of the earth. Control of this position may be either sensory or mechanical.

2. A standard swimming position may have certain mechanical and ecological advantages for the animal.

3. The most important type of mechanical orientation is probably that in which the center of gravity tends to lie below the center of buoyancy. Other mechanisms may exist which involve the lines of action of the forces of propulsion and resistance, but such mechanisms can occur only when the specific gravity of the animal exceeds (or is less than) that of the water. If there is a tendency to sink which is resisted by a vertical component of the propulsive force the animal will perhaps swim in jumps, allowing its body to be orientated by fluid pressures during the brief periods of passive sinking. When support is provided by a vertical component of the resistance

the animal may be orientated by a mechanism similar to that found in aeroplanes.

4. The various types of mechanism could be combined together in almost any way. Changes in shape shown by the swimming animal, and currents created by its own activity, may provide further complications.

5. There are a few practical methods which can be used for the study of mechanical orientation in aquatic animals, but many of the problems cannot be solved by methods known at present. Care is always required to eliminate sensory factors, and so far as possible to study the different mechanical factors isolated from each other.

6. Sensory reflex control of the swimming position may depend on a response to light, or on a response to gravity perceived by statocysts. If proprioception sometimes plays a part, the stimulus would probably be provided by the downward pressure of freely movable internal organs or liquids. Occasionally a surface sensitivity to currents could serve to control the orientation during downward sinking, or in response to "echo currents."

7. A knowledge of the mechanical factors which may control dorso-ventral orientation can also be of importance in the study of antero-posterior orientation ("taxes") and of such subjects as floatation and cyclomorphosis.

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LIST OF LITERATURE

- ALVERDES, F. 1927. Die Raumorientierung der Cloëon-Larve. *Z. vergl. Physiol.*, 5: 598-606.
- BAWDEN, F. C., N. W. PIRIE, J. D. BERNAL, and I. FANKUCHEN. 1936. Liquid crystalline substances from virus-infected plants. *Nature, London*, 138: 1051-52.
- BECK, K. 1912. Untersuchungen über den statischen Apparat von Gesunden und Taubstummen. *Z. Sinnesphysiol.*, 46: 362-78.
- BETHE, A. 1894. Ueber die Erhaltung des Gleichgewichts schwimmender Tiere. *Biol. Zbl.*, 14: 95-114 and 563-82.
- . 1895. Die Otocyste von *Mysis*. Bau, Innervation, Entwicklung und physiologische Bedeutung. *Zool. Jahrb. (Anat.)*, 8: 544-64.
- . 1910. Notizen über die Erhaltung des Körpergleichgewichts schwimmender Tiere. *Festschr. R. Hertwig*, 3: 81-92.
- BORELLI, G. A. 1681. *De Motu Animalium*. Rome. (For German translation of part on flight and swimming see Ostwald's "Klassiker der exakten Wissenschaften," Nr. 221. 1927).
- BREDER, C. M., JR., and J. E. HARRIS. 1935-6. Effect of light on orientation and stability of young plectognath fish. *Carnegie Inst. Wash. Publ.* 452. *Papers Tortugas Lab.*, 29: 23-36.
- v. BUDDENBROCK, W. 1914. Über die Orientierung der Krebse im Raum. *Zool. Jahrb. (allg. Zool.)*, 34: 479-514.
- . 1937. Grundriss der vergleichenden Physiologie. 2. Aufl., Bd. I. Borntraeger, Berlin.
- COKE, R. E. 1939. The problem of cyclomorphosis in *Daphnia*. *QUART. REV. BIOL.*, 14: 137-48.
- DEMBOWSKI, J. 1929. Die Vertikalbewegungen von *Paramecium caudatum*. I. Die Lage des Gleich-

- gewichtscentrums im Körper des Infusors. *Arch. Protistenk.*, 66: 104-32.
- . 1931. Die Vertikalbewegungen von *Paramaecium caudatum*. III. Polemisches und Experimentelles. *Arch. Protistenk.*, 74: 153-87.
- DEMOLL, R. 1909. Über die Augen und die Augensielreflexe von *Squilla mantis*. *Zool. Jahrb. (Anat.)*, 27: 171-212.
- DYKGRAAF, S. 1933-4. Untersuchungen über die Funktion der Seitenorgane an Fischen. *Z. vergl. Physiol.*, 20: 162-214.
- EYDEN, DORA. 1923. Specific gravity as a factor in the vertical distribution of plankton. *Proc. Camb. Philos. Soc. (Biol. Sci.)* [contin. as *Biol. Rev.*], 1: 49-55.
- FoxON, G. E. H. 1936. Orientation of *Chirocephalus* and *Daphnia*. *Nature, London*, 137: 948-49.
- FRAENKEL, G. 1928. Über den Auslösungsreiz des Umdrehreflexes bei Seesternen und Schlangensterne. *Z. vergl. Physiol.*, 7: 365-78.
- GRAHE, K. 1926. Die Funktion des Bogengangsapparates und der Statolithen beim Menschen. *Hdb. norm. path. Physiol.*, 11: 909-84.
- HARRIS, J. E. 1936. The rôle of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). *J. Exp. Biol.*, 13: 476-93.
- . 1937. The mechanical significance of the position and movements of the paired fins in the Teleostei. *Carnegie Inst. Wash. Publ.* 475. *Papers Tortugas Lab.*, 31: 171-89.
- . 1938. The rôle of the fins in the equilibrium of the swimming fish. II. The rôle of the pelvic fins. *J. Exp. Biol.*, 15: 32-47.
- HERTER, K. 1927. Reizphysiologische Untersuchungen an der Karpfenlaus (*Argulus foliaceus*). *Z. vergl. Physiol.*, 5: 283-370.
- JACOBS, W. 1935. Das Schweben der Wasserorganismen. *Ergebn. Biol.*, 11: 131-218.
- JAMES, W. 1887. The sense of dizziness in deaf mutes. *Amer. J. Otolology*, 4: 239- [Cited from Nagel, *Hdb. Physiol. Menschen*, 3. Vieweg, Braunschweig. 1905.]
- LAMB, H. 1924. Hydrodynamics. Fifth Edition. Univ. Press, Cambridge.
- LANGENBUCH, R. 1928. Über die Statocysten einiger Crustaceen ... etc. *Zool. Jahrb. (allg. Zool.)*, 44: 575-622.
- LEONTJEW, H. 1928. Zur Biophysik der niederen Organismen. IV. Mitteilung: die Bestimmung des spezifischen Gewichts der Plasmodien und Sporen bei den Myxomyceten. *Z. vergl. Physiol.*, 7: 195-200.
- LOWNDES, A. G. 1937. Body orientation in Crustacea. *Nature, London*, 140: 241-42.
- . 1938a. Density of living aquatic organisms. *Nature, London*, 141: 289-90.
- . 1938b. The density of some living aquatic organisms. *Proc. Linn. Soc. London*, 150: 62-73.
- LUNTZ, A. 1929. Weitere Untersuchungen über die Sinkgeschwindigkeit von Süßwasserorganismen. *Zool. Jahrb. (allg. Zool.)*, 46: 465-82.
- MAGNAN, A. 1929. Les caractéristiques géométriques et physiques des poissons, avec contribution à l'étude de leur équilibre statique et dynamique. *Ann. Sci. nat. (Zool.)*, (10), 12: 5-136.
- . 1930. Same title. *Ann. Sci. nat. (Zool.)*, (10), 13: 355-489.
- MAGNUS, R., and A. DE KLEIJN. 1930. Körperstellung, Gleichgewicht und Bewegung bei Säugern. *Hdb. norm. path. Physiol.*, 15, 1: 29-54.
- v. MISES, R. 1936. Fluglehre. Vorträge über Theorie und Berechnung der Flugzeuge in elementarer Darstellung. 5. Aufl. Springer, Berlin.
- MÜLLER, R. T. 1918-19. Tanymastix lacunae (Guérin) aus dem Eichener See (südl. Schwarzwald. *Z. Biol.*, 69: 141-274.
- OEVERMANN, H. 1936. Das statische Verhalten einiger Wasserwanzenarten. *Z. wiss. Zool.*, 147: 595-628.
- OSTWALD, W. 1903. Zur Theorie der Schwebvorgänge sowie der spezifischen Gewichtsbestimmung schwebender Organismen. *Arch. gesamt. Physiol.*, 94: 251-72.
- PARKER, G. H. 1922. The geotropism of the sea urchin *Centarchinus*. *Biol. Bull.*, 43: 374-83.
- PARR, A. E. 1927. Keeling sick fishes. *Bull. New York Zool. Soc.*, 30: 66-67.
- PLATE, L. 1924. Allgemeine Zoologie und Abstammungslehre. Zweiter Teil: Die Sinnesorgane der Tiere. Fischer, Jena.
- PLATT, JULIA B. 1899. On the specific gravity of *Spirostomum*, *Paramaecium*, and the tadpole in relation to the problem of geotaxis. *Amer. Nat.*, 33: 31-38.
- RÁDL, E. 1901. Über den Phototropismus einiger Arthropoden. *Biol. Zbl.*, 21: 75-86.
- RIZZOLO, A. 1929. A study of equilibrium in the smooth dogfish—*Galeus canis* (Mitchill). *Biol. Bull.*, 56: 383-89.
- SCHLÜTER, C. 1933. Die Bedeutung des Centralnervensystems von *Hirudo medicinalis* für Locomotion und Raumorientierung. *Z. wiss. Zool.*, 143: 538-93.
- SEIFERT, R. 1930. Sinnesphysiologische Untersuchungen am Kiemenfuss (*Triops cancriformis* Bosc.). *Z. vergl. Physiol.*, 11: 386-436.
- . 1932. Raumorientierung und Phototaxis der Anostraken Euphyllopoden. (Versuche an *Chirocephalus* und *Artemia*). *Z. vergl. Physiol.*, 16: 111-84.
- TESTER, A. L. 1940. A specific gravity method for determining fatness (condition) in herring (*Clupea pallasii*). *J. Fish. Res. Board Canada* (formerly *Biol. Board*), 4, 461-71.

- TOWNSEND, GRACE. 1939. A vibration sense in a swarming annelid. [Abstract]. *Biol. Bull.*, 77: 313.
- WESENBERG-LUND, C. 1908. Plankton-Investigations of the Danish Lakes. II. *Kopenhagen*.
- WILLIAMS, S. R. 1900. The specific gravity of some fresh-water animals in relation to their habits, development, and composition. *Amer. Nat.*, 34: 95-108.
- WOJTUSIAK, R. J. 1929. Über Lichtreaktionen normaler und geblendeter *Acilius*-Larven. *Acta Biol. exp. Warszawa*, 3: 165-74. [Cited from *Ber. wiss. Biol.*, 12: 684. 1929.]
- WOLF, E. 1925-6. Physiologische Untersuchungen über das Umdrehen der Seesterne und Schlangensterne. *Z. vergl. Physiol.*, 3: 209-24.
- WOLTERECK, R. 1913. Über Funktion, Herkunft und Entstehungsursachen der sogen. "Schwebefortsätze" pelagischer Cladoceren ... etc. *Zoologica, Stuttgart*, 26: 475-550.





THE PITUITARY BODY IN GIANT ANIMALS FOSSIL AND LIVING: A SURVEY AND A SUGGESTION

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WHEN G. Elliott Smith, comparative anatomist of the brain, in his description of an endocast of the cranial cavity of a giant Moa briefly remarked "The hypophysis is very large" (1902), little was yet known of the relation of the pituitary gland to body size. Nor could F. Nopcsa, the palaeozoologist, realize the full implications when he demonstrated that the fossa hypophyseos is larger, in relation to the brain cavity proper, in giant dinosaurs than in their smaller relatives (1917). For the definite proof of the influence of the pituitary gland on body growth, the separation, from the many other substances produced by the gland, of the anterior lobe growth hormone, was not achieved until 1921 (H. M. Evans).

I. PITUITARY GLAND AND BODY SIZE: SOME ESTABLISHED FACTS

Pathology

The normal growth-regulating function of the pituitary body (PB) was first inferred from its disturbances in man. Human growth disturbances were found to be accompanied by abnormal PBs: dwarfs suffer from hypopituitarism, abnormally tall men from hyperpituitarism. The latter disease occurs in two forms. In acromegaly, the sella turcica of the sphenoid bone is enlarged (in 93 per cent of cases) by a tumor in which the acidophilic secretory cells of the anterior pituitary lobe are increased. In human giantism, in contrast to acromegaly, intensive growth starting before or during adolescence produces a well-proportioned abnormally tall skeleton; hyperplastic changes in the anterior pituitary lobe widen, lengthen, and deepen the sella.

While we know that size variations occurring normally in nature tend to "mendel back" to medium size (unless selected by breeders), clinicians have found family predisposition to pituitary diseases; for example, three sisters and a brother described by J. Bauer were normally built giants of 190, 185 and 183 cm. in height and an achondroplastic dwarf of 121 cm. Geneticists also have ascertained a linkage between defective development of the animal PB and the inheritance of structural distortions (Stockard, in *The Pituitary Gland*, cf. Bibliography).

Experiments

Animal experiments have shown that, when the pituitary body is removed, growth stops altogether and cannot be revived by any kind of medication, whereas the slowing down of growth in thyroidectomized animals is entirely cured by treatment with anterior lobe extracts (Evans, in *The Pituitary Gland*). Natural dwarfs occurring in Evans' rat colony were always restored to complete normality by administration of the growth hormone (Evans *et al.*, '33).

In the normal rat, the response of the bones to injections of anterior lobe extract is an overstimulation of normal periosteal growth (cf. for example, Evans, Handelsman). Injected rats become twice as heavy as the controls; some of them surpass the normal maximum size of the species. The absence of acromegalic stigmata in these giant rats has been attributed to the fact that in rats the bone epiphyses never unite (Putnam, in *The Pituitary Gland*). This assumption is based on the disputed doctrine that giantism is the acromegaly of youth. Experiments with various breeds of dogs tend to show (if conclusions

may be drawn from the reaction of so few individuals) that racial constitution decides the result of experimental hyperpituitarism. An English bulldog grew to almost twice the weight of litter-mate controls through anterior lobe injections; growth, however, was not evenly distributed but typically acromegalic (Putnam *et al.*). In dachshunds, symmetrical overgrowth = giantism occurred consequent on injections, the only outstanding acromegalic feature being folded skin (Evans *et al.*). In sheep-dogs likewise, no difference of the skeletons was observed, apart from size, between an experimental giant of 30 kg. and its litter control of 20 kg. weight (Evans *et al.*).

Hypophysectomized chick embryos never reached the size of controls of the same age (Fugo). As far as the writer is aware, none of the records of pituitary injection experiments on birds, nor any report on reptile experiments mention the animals' size. In the case of the sauropsids, therefore, palaeontological data (see below) fill an actual gap in the chain of proofs of the rôle played by the PB in conditioning body-size—already decisive enough, however. A diet of cattle anterior lobe not only increased the rate of growth in *Amblystoma*, but these newts never ceased to grow after reaching the normal maximum size of the two species used in Uhlenhuth's experiments.

Relative size of the pituitary body

In endogenous giants, the size of the PB was stated above to vary in direct proportion to the amount of secretion. This applies not only to human pathological cases but may become apparent in normal size variation. In the larger breeds of cattle, and in the larger individuals within a breed, the PB is larger in relation to body size than in smaller ones (Petersilie). A moderate positive correlation exists between the weight of the PB, but particularly of the anterior lobe, and body size in the normal adult human (Rasmussen, in *The Pituitary Gland*). Large human skulls have in general larger sellae turcicae than small skulls (Kadanoff). In the exogenously developed experimental giants the PB is, of course, not, or hardly, enlarged, supply from outside replacing hypersecretion. The foxhound bitch injected by Benedict *et al.* grew to 150 percent the weight of its sister, yet the increase in PB weight was only 7 percent; uterus and ovaries were 300 percent, thyroid and spleen, 100 percent heavier; the difference in brain weight amounted to no more than 3 percent.

We are here facing a phenomenon which has an extremely important bearing on our present investigation: the fact that brain growth follows other laws than body growth and PB growth.

Experimental proofs thereof are abundant. Mortimer, investigating only the skulls of young rats after hypophysectomy, observed that snout growth is more impeded than the development of the brain case, and that post-operative treatment with growth hormone produces satisfactory growth only in the snout. In the giant rats produced by the experiments of Rubinstein (in *The Pituitary Gland*), the brain was always smaller in relation to body size than in normal rats. Rubinstein's extensive experimental and mathematical investigation definitely showed that the growth hormone, while markedly stimulating body growth, fails to affect the growth or structure of the central nervous system.

The palaeontological aspect

This only confirms the palaeozoologists' experience of phylogenetic increase in body size. The comparative anatomist too is, of course, well aware that the brain and neurocranium of a larger animal are smaller in relation to body size than those of its smaller congener. The palaeontologist sees the neurocranium actually lagging behind during phylogenetic increase of body size, as a rule, and always in the evolution of definite giants.

The recent achievements of medicine and experimental zoology now reveal the seat of the force which must have promoted phylogenetic body growth as it does ontogenetic growth. They enable the palaeontologist to investigate, as directly as is possible within his realm, the growth organ itself, and to check the development of its size—that is, its power—with that of the brain even where only skulls are preserved.

Due to its complex origin, the pituitary, master among endocrine glands, is, so to speak, directly accessible to palaeo-anatomical investigation. The PB is lodged in the brain case because its "posterior lobe" (posterior in man) is its pars nervosa, the neurophysis, ontogenetically a downward diverticulum from the floor of the diencephalon. Yet it lies below the brain case proper and may be provided with its own capsule by the sphenoid bone (the sella turcica in man), because its epithelial portion, the hypophysis s. str. ("anterior lobe" = pars glandularis, etc.) is a pars buccalis, ontogenetically the terminal part of an upward

diverticulum from the dorsal side of the roof of the mouth.

Until now, however, apart from dinosaur giantism only one phylogenetic trend has been interpreted in terms of hyperpituitarism: Keith found that the differences between *Homo sapiens* and *Homo primigenius* are mainly the latter's acromegalic symptoms! This view had also been taken by Larger, but he emphatically denies the connection between PB and *l'acromégalie-gigantisme*. In vain the palaeozoologist searches neozoological literature for data of animal PBs with reference to the formation of their specific body size (except for the papers of Robb and Rost discussed below); nor have any investigators of animal and human PBs taken into account the palaeozoological facts referred to in our introductory sentences. Yet normal animals, living and extinct, testify plainly to the phylogenetic significance of the pathological, statistical, and experimental observations which may be summarized as follows:

(1) Body-growth, but apparently not brain growth, is dependent upon the amount of growth hormone produced by the anterior lobe of the PB. (2) More hormone is produced by large glands than by small ones. (3) Hyperpituitarism enlarges the sella turcica. (4) Tendency to hypo- and hyper-pituitarism is hereditary. (5) Hyperpituitarism can produce animals above maximum normal size.

II. REPTILES

[No Anamnia have been studied with regard to our subject. Enlightening differences might be revealed by comparisons of the PB of giant fish with that of smaller congeners such as a 450 kg. *Thunnus* and an 8 kg. *Neothunnus*. Likewise, there doubtless exist differences between the PB of small frogs and that of the 30 cm.-long *Rana goliath*; in Herrick's figures of the middle sections of brains of adult *Amblystoma tigrinum* (maximum body size 27 cm.) and *Cryptobranchus alleghaniensis* (55 cm.), I find the glandular lobe of the PB less than half as long as the tectum mesencephali in the smaller but exactly as long as the tectum in the larger newt.]

There are giants among the living reptiles such as 5 m.-long snakes, 2 m.-long turtles, and 3 m.-long lizards; their PBs remain to be studied, and to be compared with those of the small representatives of these orders. The size of lizard PBs should, furthermore, be compared with the volume of the

pituitary fossa of 8–10 m.-long mosasaurs: this pouch in the skull base was the bony capsule of the PB and thus reproduces approximately the size of the long-vanished gland. Some reptiles, however, are excluded from palaeoendocrinological investigation by the fact that only the distal extremity of their PB lies in no more than a trough-like depression on the sphenoid bone. In others, the fossa may retain its embryonic condition, that is, remain open across the entire sphenoid bone. Thus, the ichthyosaurs should prove particularly favorable objects for comparative investigation. It appears that this could be undertaken on intact skulls. A widely open cranio-pharyngeal canal penetrates the basisphenoid of some ichthyosaurs. Endocasts of this canal might exhibit illuminating differences between specimens of different size; the outside opening has been found in the largest known (2 m.-long) *Ichthyosaurus* skull as well as in smaller specimens. The pituitary space proper is a well-marked expansion within the cranio-pharyngeal canal of the giant dinosaur family *Atlantosauridae* of which it is believed that this persistent communication between the brain and mouth cavities was a family character. (O. C. Marsh: for literature on fossil brain cavities see lists in Edinger, 1929 and 1937.)

It is, of course, no mere coincidence that the only animals so far described as having, so to speak, disproportionately large pituitary fossae are the giants par excellence—the dinosaurs. In Jurassic sauropod skulls, the 25 m.-long but slimly built *Diplodocus* shows a slender sac below the brain case as deep as this is high; in the stouter 17 m.-long *Camarasaurus*, the lower part of the sac has a much greater diameter than the upper (Fig. 1): the “anterior lobe” of the PB being ventral to the other parts in reptiles. Apart from the fossae of giant sauropods which he briefly characterized as *ungeheuer* (monstrously large), Nopcsa investigated the fossae of seven small and seven large dinosaur genera. This enabled him to restrict direct comparison to genera of established ancestry. His interpretation of *dinosaur giantism as being the result of an increase in pituitary function* is therefore based on the, so to speak, actual observation of a process, namely that “bei diesen Tieren im grossen und ganzen mit der Zunahme der Körpergrösse eine Zunahme der Hypophyse ihrem Hirn gegenüber Hand in Hand geht . . . die Grösse des Hirnschädels bleibt dabei stationär.” This means that, in dinosaurs, phylogenetic increase in body-size was accompanied by

an increase in size of the PB, while brain size remained the same. The many endocranial casts of dinosaurs now known prove the basic truth of Nopcsa's ('17) doctrine.

Brown and Schlaikjer note among the differences between the endocranial cast of the primitive small ceratopsian *Protoceratops* from the Mongolian Upper Cretaceous and that of the large advanced *Anchiceratops* from the American Upper Cretaceous ('40, p. 192) that the PB in the former is "relatively small and narrow," in the latter, "relatively large and broad." Dr. Brown very kindly allowed the present writer to examine the

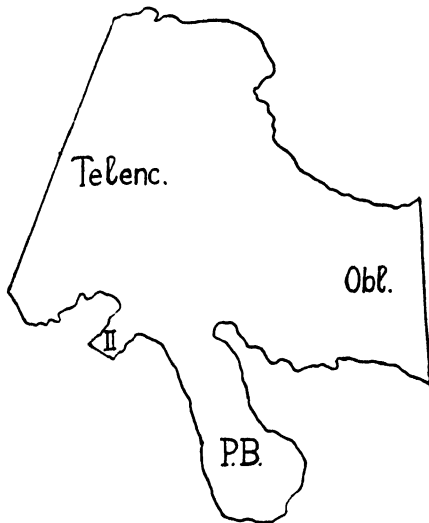


FIG. 1. OUTLINE OF ENDOCAST OF BRAIN CAVITY OF CAMARASAURUS SUPREMUS

From left side, after Osborn. Two-fifths natural size. Telenc.: cast of caudal portion of forebrain chamber. Obl.: cast of medulla oblongata chamber. II: cast of optic nerve canal. PB: cast of fossa pituitaria.

two endocasts. The length of the brain case, from the notch between the olfactory and optic nerve foramina to the foramen magnum, was found to be 65 mm. in *Protoceratops* and 72 mm. in *Anchiceratops*. Brain length, however, measured from that notch to the posterior end of the cerebellum, was exactly the same in the small and the large forms, viz., 49 mm.: only the medulla oblongata was more voluminous in the giant. The *Protoceratops* skull from which the cast was taken is 611 mm. long. The only complete *Anchiceratops* skull is 1660 mm. long but is from a smaller individual than that which furnished the cast (Sternberg). On the other hand, the difference

between the casts of the pituitary fossae is indeed very striking. Both are well set off from the brain cast proper by a stalk. Their greatest lengths, breadths and heights are: *Protoceratops*, 13, 11, 21 mm.; *Anchiceratops*, 14, 21, 37 mm. While in *Protoceratops* the pituitary fossa tapers in breadth and length and its cast is a pointed wedge, that of *Anchiceratops* retains the same breadth and length almost to the lower extremity.

Exact data on the relative sizes of brain case and pituitary fossa in dinosaurs have been given by Janensch ('35)—data which are not known of any living animal. Janensch was able to study several brain casts of three Jurassic sauropod genera, the entire skeletons of each of which were known to him and, in one instance, even that of the very individual which furnished a cast. This was a representative of those greatest giants which ever trod the earth, viz. the genus *Brachiosaurus* which could raise its head 12 m. above the ground; the body reached 25 m. in length, and some 50 tons in weight.

Janensch estimates the body of his specimen in life at 25 cubic meters. It has a brain cavity proper of 309.5 cubic cm. and a fossa hypophyseos 13.8 ccm. = 4.5 percent of the brain cavity. In a smaller *Brachiosaurus* skull, the proportion is $198.2:15.2 = 7.4$ percent. In the smaller genus *Barosaurus*, in an individual the body of which was estimated at 15 cubic meters, a brain cast of 198.8 ccm. had a much larger hypophyseal appendage—18.5 ccm. = 9.4 percent. Within the species, however, the smaller the skull, the smaller the relative size of the PB was found to be—for instance, 9.2 ccm. = 7.6 percent of the 120.8 ccm. brain cavity. In the still smaller *Dicraeosaurus* (skeleton-length 13.20 m.), the numbers, including a parietal sinus of the brain cavity, are $194:14 = 7.2$ percent; excluding the sinus, $140.8:14 = 9.9$ percent.

These figures prove that there existed a tribe of animals in which the PB was so large that the volume of its capsule was as much as $\frac{1}{10}$ of the brain case volume. This was the group which contained the largest terrestrial animals ever known.

Pointing to the prevalent sterility in human giants and acromegals, Nopcsa suggested that hyperpituitary decrease of sex functions, along with the general decrease of natural resistance in any giant body, was the cause of extinction of the sauropods. In our opinion, Nopcsa goes too far in stressing the parallel between

the normal dinosaur giantism and the human hyperpituitary diseases. Particular objections spring from two standpoints:

1. The sauropods flourished for many millions of years after reaching giant size. Abundant up to the end of the Cretaceous period, they then disappeared together with practically all characteristically Mesozoic phyla, small and big.

2. The anterior pituitary lobe itself also produces a sex hormone, and this normally prevails over the growth hormone in the adult. Sexual dysfunction in hyperpituitary women has been observed by Henderson to occur only when the sella turcica is considerably enlarged by an adenoma of the PB. This pathological growth compresses the cells which elaborate the hormones controlling sex function, but it does not destroy them. After operations with radical extirpation of the adenoma, Henderson found that the normal menstrual cycle was resumed and pregnancy occurred. The enlargement of the dinosaur fossa hypophyseos, however, was normal. Animal experiments too have shown that certainly not every kind of hyperpituitarism causes sterility. Experimental administration of cattle anterior lobe, even though disturbing the sexual rhythm in young rats, has increased sex activity in senile rats, caused hens to lay more and larger eggs, produced hypertrophy of the gonads in young alligators, and stimulated the ovaries of frogs.

III. BIRDS

The general remark in the *Handbuch der Zoologie* on the avian PB, "*wenig entwickelt*" (Stresemann, p. 107), calls for correction. Kuenzi's comparisons of the brain-part surfaces throughout the bird system showed that the PB is relatively small, for instance, in sparrows, rather large in fowl, and very large in the ratites.

The greatest body-size also is attained by the earth-bound ratites. The largest ostriches reach 260 cm. body-height; the largest flying bird, the albatross, 116 cm.

Flightless types in various euornithid orders also developed giant forms. The largest living penguin, the emperor, stands 1 m. high. Its PB should be investigated together with that of a small penguin. A Miocene penguin was twice as large as the emperor penguin. Its skull, however, is still unknown, and so is the skull of an Eocene ground-bird of fourfold ostrich-height.

The largest ratite genera are also extinct. Complete skeletons have been mounted from medium-sized bones only, not from the largest. That of a *Dinornis maximus*, the New-Zealand Moa, is 255 cm. high; one of the Madagascar *Aepyornis maximus*, 300 cm.

Now the very strata which contain the remains of these subfossil heavy giants have also furnished remains of smaller, lighter-built representatives of the respective families to which the giants belong, down to the size of a turkey. It is obvious that the smaller forms, although they lived together with the giants, are less advanced types. They are therefore considered the ancestral forms (Lambrecht), and we here possess evidence of *development of giantism within families*. Since the avian brain is so tightly fitted into the skull that endocasts furnish exact replicas of the brain form, and since the avian PB, set well off the brain by its long stalk, is encased in a separate bony chamber, the two ratite families furnish excellent tests of the problem we are concerned with.

Dinornithids

We have said that Elliot Smith was struck by the size of the PB in the Moa. Owen, too, who first described the brain of *Dinornis maximus*, had remarked in 1872: "The hypophysis, as represented by the cast of the sella, is of considerable size." The significance of this becomes apparent when the *Dinornis* endocast (Royal College of Surgeons, London, catalogue number D. 148) is compared with an endocast of the smaller dinornithid *Anomalapteryx* (Senckenberg Museum, Frankfurt a.M., Av. 29 a).

Not having sawed skulls at hand in which to measure the interior spaces, and not being able to take volumetric measurements on the plaster casts or to apply a formula to those differently shaped parts of the casts, the writer took recourse to a simple method feasible for comparison, though inaccurate as to absolute size. The three diameters of the PB casts were multiplied with each other, and so were those of the forebrain casts (the form of which, unlike that of other brain parts, is similar in both families investigated). The imaginary cubes, of course, suggest volumes larger than are actually present either in the wedge-shaped or globular PBs or the heart-shaped forebrains. As, however, they are only computed for the sake of comparison with each other, the relative figures at which we are finally aiming, the proportion of the cubes, cannot be far from the true proportions of PB and forebrain. Indeed, Rost calculated the volume of the PB in two races of pigeon by addition of section superficies as well as by multiplication of the diameters of the PB and, in spite of the difference in the resulting absolute numbers,

found practically the same inter-racial ratio by both methods, namely, 1:1.414 and 1:1.49, respectively.

In *Anomalapteryx didiformis*, the diameters of the PB are 8.5, 7, 8 mm., the cube, 476 cmm.; the telencephalic cube is 29.500 cmm. The proportion of PB size to forebrain size, therefore, is 1:62 (1:67 in the ostrich endocast RCS, D 155). In *Dinornis maximus*, the figures are 12 x 12 x 14 mm. = 2016 cmm. and 68.880 cmm.: the proportion is 1:34. In relation to forebrain size, the pituitary body of *Dinornis* thus is found to have had almost twice the size of an *Anomalapteryx* PB. The ratio *Anomalapteryx:Dinornis* is: body height, 1:2.1; forebrain volume, 1:2.2; but PB volume, 1:4.2.

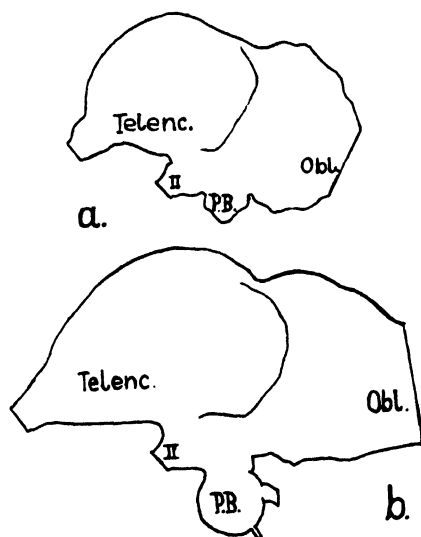


FIG. 2. OUTLINES OF ENDOCRANIAL CASTS OF (a) MULLERORNIS AGILIS (b) AEPYORNIS MAXIMUS

Left side views, two-thirds natural size. In (b) the cranio-pharyngeal canal is seen to open into the pituitary fossa from below, the carotid artery canal from behind.

Aepyornithids

It is true that we do not know the size of the individuals which furnished endocasts of brain cases either in the dinornithids or the aepyornithids. However, the author's investigation of 6 aepyornithid brains belonging to 4 species (Edinger '42) showed that two brains of one species are almost exactly alike, in spite of the size variability within aepyornithid species. Only one brain of each species was complete with PB.

Seen from above, these casts are rather similar to each other and to ostrich brains. The lower

side reveals striking differences: the PB of the ancestral genus *Mullerornis* is the size of a blueberry (384 cmm.), that of the largest *Aepyornis* species, *A. maximus*, is the size of a cherry (3038 cmm.). The PB volume compares to the forebrain volume, with rising body size, as follows: *Mullerornis*, 1:102; *Aepyornis hildebrandti*, 1:82; *Aepyornis medius*, 1:36; *Aepyornis maximus*, 1:24!

When reading the table of interspecific ratios given in Table 1 (computed from numbers to be published in Edinger '42), the following points should be born in mind:

1. Below the stalk, which is not included in the measurements taken, the PB of *Aepyornis maximus* bulges out to form a globe, while those of *Mullerornis* and the smaller *Aepyornis* species are somewhat flattened antero-posteriorly; that is, the computation of the "cube" exaggerates the size of the PB more in

TABLE 1
Interspecific ratios

	BODY- HEIGHT	FORE- BRAIN- VOLUME	P.B.- VOLUME
<i>Mull.:Aep. hild.</i>	1:1.1	1:1.6	1:2.0
<i>Mull.:Aep. med.</i>	1:1.4	1:2.0	1:5.6
<i>Mull.:Aep. max.</i>	1:1.7	1:1.8	1:8.0
<i>Aep. hild.:med.</i>	1:1.3	1:1.2	1:2.8
<i>Aep. hild.:max.</i>	1:1.6	1:1.1	1:4.0
<i>Aep. med.:max.</i>	1:1.2	1:0.9	1:1.4

the case of the smaller species than in the giant, the relative PB volume of which would therefore appear even larger had the actual volumes been measured.

2. The body-heights are two-dimensional measurements and their comparison does not express the increase in body-volume in the evolution of the aepyornithids; this, naturally, was greater. However, height-comparison throws more light on the respective body-volume of these animals of identical build, with so small a trunk between such enormous legs and neck, than it would in almost any other animal. The numbers in the first column of the table rely on no more than the following mounted skeletons:

Mullerornis agilis: Tananarive (Madagascar), 148 cm.

Aepyornis hildebrandti: Tananarive, 165 cm.; London (England), 158 cm. = ~ 160 cm.

Aepyornis medius: no skeleton mounted; 211 cm. was computed from medium height of *Aep. max.* by the proportion of the medium tibiotarsus lengths of the two species.

Aepyornis maximus: Tananarive, 221 cm.; Paris (France), 300 cm. = ~ 260 cm.

These figures are so striking that we may draw the following conclusions although they are based on but one brain case of each species:

With increasing body-height in aepyornithid birds, the forebrain volume increases at a slightly higher rate than does body-length (but presumably at a lesser rate than does body-volume) only when the primitive genus is compared with the advanced genus. Within the genus which developed giantism, forebrain increase stays behind increase in body-height. Meantime the PB increases at a much greater rate than does the body, manifesting almost 4½-fold the increase of forebrain volume in a comparison between the small genus and the largest giant species.

Manifold though the activities of the PB are, the evolutionary trend in aepyornithids shows that this hyper-development of the PB was connected with their natural giantism. Even without the possibility of histological examination we are entitled to assume that the striking enlargement of these fossil pituitary fossae was due to an enlargement of the glandular lobe of the long-vanished PB.

Characters of subfossil ratites other than size likely to be due to hyper-activity of the PB

It has long been known that the volume of eggs of all *Aepyornis* species, above and below ostrich size, is much larger than that of ostrich eggs. The diameters of *Aepyornis* eggs are 280–340 and 213–245 mm., those of ostrich eggs 150–155 and 110–130 mm. This now proves to be a natural parallel, on a grand scale, to the effect on eggs of experimental hyperpituitarism: the eggs of pituitary-fed hens were over ½ heavier and ½ larger than the eggs of controls (Gutowska).

Together with their usually large size, there is one other characteristic distinguishing ratites from flying birds which is influenced by pituitary hormones—their plumage. Plumage development is controlled by the thyroid, the action of which, however, is regulated by the PB. Hypophysectomy in adult pigeons was followed by heavy moulting (Hill); the feathers of chickens hypophysectomized as embryos were shorter and less well developed, their sheaths were thicker and tougher and did not release the barbs as easily as in controls (Fugo). Implantation of anterior lobe stimulated feather regeneration (Voitkevich). Likewise, in human pathology, reduction of pituitary function causes loss of hair, while increase in hair-thickness and of the areas of hair-distribution

(hypertrichosis) is observed in more than half the cases of giantism and acromegaly. Thus the fact that *Dinornis*, according to the numerous pits for feather insertion found in the metatarsal integument, must have been feathered down to the toes (Owen, 1883), and the peculiar “hair-likeness” and luxuriance of the plumage of the large ratites, now appear as a natural parallel to human hyperpituitary hypertrichosis. The looseness of the ratite feather barbs obviously is a natural counterpart to Fugo’s experiment. The plumage of the aepyornithids is not known, but feathers of *Dinornis* have been found; they are soft, their barbs do not cling together to form a vane but are loose, filamentary: just the opposite to the feathers of Fugo’s hypophysectomized chicken.

From the ecological viewpoint, this kind of feather is just one of the characteristics of birds unable to fly, and so is their size. How very far we are from being able to discriminate cause and effect, from knowing what is primary and what is secondary, is obvious from the existence of Lowe’s doctrine according to which the ratite type is primitive, and branched off the main bird stem before flight was developed. If this were so, then, from the standpoint of the present investigation, we certainly could not consider the ratite feathers as signs of a kind of pituitary “disturbance” for they would be primitive, no “Zuruecksinken auf den Typus der Halbdune” (Stresemann). While agreeing with Romer’s ecological interpretation of the origin of flightless birds, namely, that birds were liable to return to ground life in areas free from enemies (that is, areas in which extravagant hyperpituitarism and hypopituitarism (island dwarfs!) could also develop without immediately endangering the species), we note that no less an ornithologist than Stresemann forms just the reverse conception. In his opinion, the loss of the power of flight was the inevitable consequence of increase in body-size. From our point of view, this would mean nothing less than that the development of the ratite bird type was due to the activity of the pituitary gland!

Wiman (see Edinger and Wiman) has discovered a canal running from the nethermost pit of some *Aepyornis* (but no *Mullerornis*) pituitary fossae downwards and slightly backwards to the palate. The “venous foramen” on the lower side of the basisphenoid and the “mid-vertical canal” described and figured by Owen (1879, p. 263, 272, 280) in three *Dinornis* species show that such

persistence of the cranio-pharyngeal canal occurred in the other subfossil giant ratite family too. There is no record of this feature in other birds. Jaekel's search for the cranio-pharyngeal canal in present-day reptiles succeeded in discovering it only in three individuals; it may be significant that these were one alligator, one turtle of the large species *Chelone midas* whose shell reaches 130 cm. in length, and one lizard of the largest tejid species *Tupinambis teguixin* which is almost 1 m. long. We mentioned above that this embryonic character was retained in the largest-known, thus doubtless hyperpituitary, *Ichthyosaurus* (according to Fraas: *Gefässkanal*, p. 15), but also in "smaller" *Ichthyosauri* which, however, would have been considered giant reptiles had they lived to-day. It is certainly striking that the same is the case in Plesiosaurs. The basisphenoid foramen described by White ('35) in the largest known plesiosaurian, the 372 cm.-skull of *Kronosaurus*, exactly corresponds to the pharyngeal opening of the canal descending from the ichthyosaurian fossa hypophyseos, and so does this foramen in the 68 cm.-long skull of *Macropylus* (White '40). As "extraordinary, . . . unique for *Trinacromerum* and *Polycotylus* among Plesiosaurs" this same foramen had been mentioned by Williston; it thus existed in a third plesiosaurian family, in animals of 3 m. body length. A median foramen in the palate of the type skull of the largest pterosaurian, *Pteranodon ingens*, is regarded as *Hypophysenloch* by Versluys (p. 758); in my opinion, however, the position of this vacuity (in front of the orbits in an animal whose brain lies behind the orbits) forbids this interpretation. On the other hand, a persistent cranio-pharyngeal canal is observed in all skulls of one giant dinosaur family, the *Atlantosauridae*.

It thus appears that persistence of the embryonic cranio-pharyngeal canal is much more common in giant birds and reptiles than in small ones. Should more material prove this to be true, the canal might be considered another sign of sauropsid hyperpituitarism.

There is also one record of the canal in an adult giant whale (*The Pituitary Gland*, Fig. 93a). On the other hand, it follows from Cave's statistics of the occurrence of the canal in higher primates that within a non-hyperpituitary group of mammals the frequency of persistence of the canal is by no means proportionate to body-size; the canal was present in 0.2 percent of the 5000 human

skulls investigated by Cave, while the percentage in his ape material was: Orang, 14 percent; Gorilla, 35 percent; Chimpanzee, 64 percent.

IV. MAMMALS

The very name "sella turcica," derived from human osteology, indicates that the mammalian PB does not possess an actual bony capsule (and the term should not, in the writer's opinion, be applied to such fossae as are found, e.g., in birds). Not even the clinoid processes transversely bordering the laterally open "saddle" are present in every mammal. De Beer's description of the complete absence of a dorsum sellae in *Sorex* (1929: "the floor of the pituitary fossa—if it is permissible to speak of such a structure in *Sorex*—passes insensibly back into the basal plate") is rendered particularly instructive for the palaeo-endocrinologist by the addition of a list of mammalian genera exhibiting a similar state as well as a list of genera with a well-marked dorsum sellae. The former belong to the most primitive orders, Monotremata, Marsupialia and Insectivora, and to Sirenia and Edentata. The latter are Rodentia, Carnivora, Ungulata and Primates. But in the latter orders too, the palaeo-neurologist may find on the base of an endocranial cast only a low, ill-delimited protuberance representing the shallow depression in the sphenoid, upon which, rather than in which, the gland lay in the living animal. Furthermore, there are also mammals lacking any trace of a sella.

Thus, as far as Mammalia are concerned, the proposed investigation rests mainly with the zoologist. Fortunately, some information on the PB of living mammals has already been published which yields results when viewed from our present standpoint. On the other hand, a great proportion of the existing endocasts of fossil mammals was described at the time when anatomists were mainly interested in forebrain convolutions, hence they published only top-view illustrations, and scarcely mentioned a single feature of the brain base.

This is, for instance, true of the description of the endocast of the Pleistocene marsupial *Thylacoleo* (of lion's size). The specimen in the endocast-collection of the Royal College of Surgeons of England shows, however, that this giant's PB must remain unknown—only the dorsum sellae has left a mark. The case of the cranial cavity of the living *Phascolumys* is entirely flat in the

pituitary region, while that of the giant kangaroo, *Macropus giganteus*, bears a well-delimited prominence.

From the endocast of *Tillotherium*, the Eocene insectivore of bear-size, nothing but an extremely ill-defined sella can be inferred. In accordance with Wislocki's finding of extremely shallow sellae in living sloths ('38), the pituitary area is flat in endocasts of fossil Edentata; yet the Gravigrada include such contrasts as the lightly built Miocene types and the stout Pleistocene *Megatherium* of 6 m. body-length.

Some Carnivora endocasts show no distinct pituitary protuberance (*Canis*, *Ursus*, *Meles*), some an ill-delimited one (*Lutra*, *Ailuropus*), and some obviously reproduce the distinct form of the PB: *Ailurus*, and most strikingly, *Felis tigris*. This tiger's PB was 13 mm. long and 10 mm. broad. The cat's PB measures 4 x 4 x 2-3 mm. (Trautmann) and thus is no smaller relatively than the tiger's. Similarly, Robb's comparison of the PB:body-weight ratio within one living rodent species demonstrated that the same decrease in relative PB-weight as takes place during growth in the small Polish rabbit and the giant Flemish rabbit is observed in the comparison of the adult forms; the relative PB-weight is even larger in the full-grown "dwarf" than in the "giant." If, however, comparison is made between the endocasts of various rodent genera, the pituitary region is seen to be flat but for one striking exception. This concerns the most bulky living rodent, *Hydrochoerus* (1 m. long, $\frac{1}{2}$ m. high), which has, below a forebrain 65 mm. long, a pituitary protuberance 12 mm. in length.

The coin-shaped PB of the halicorid Sirenia makes hardly any impression in the flat sphenoid bone—but here too we encounter one significant exception. On endocasts of the giant seacow, the 7-10 m.-long subfossil *Rhytina*, there are slight hypophyseal elevations measuring no less than 21 x 33, 28 x 35 and 29 x 29 mm., while forebrain-lengths are 120-123 mm.

One of the few differences between the endocranial casts of the Eocene oldest sirenian and oldest proboscidean genera is that the latter has a prominent PB 14 x 9 x 4 mm. In the endocast of an *Elephas*, however, the pituitary region is indistinctly modelled. From a figure of an elephant brain (Smith '02), PB length and breadth have been measured at 40.3 and 24.5 mm. respectively. Likewise, Wislocki ('39) found the

diameters of the PB of an adult Indian elephant 42 x 26 x 12, and he states that the proportion of its 7.53 g. weight to body-weight is no larger than in the hog (0.0002 percent = 1:50,000). But in the present context it appears significant that the neural lobe is very much smaller than the glandular lobe, their weight-ratio being 1:8.4. The only other record on the elephant PB is macroscopical only and refers to a 25-day-old calf (Dexler '07); the diameters are 24 x 16 x 6.

In a survey of the Roy. Coll. Surg. ungulate endocasts, the size of the pituitary protuberance in *Hippopotamus* at once strikes the eye. Its diameters are 27 x 25 x 17 mm. (forebrain-length 117 mm.), while the base of a *Sus scrofa* cast, with a forebrain of 86 mm. in length, is quite flat and unaffected by the gland, which measures in the pig 8-10 x 7-8 x 6-7 mm. (Trautmann). Most endocasts of artiodactyls bear some impression of a sella, but again that of a giant—the Pleistocene giant deer, *Megaceros*—is arresting for its distinctly modelled, large pituitary protuberance; this has a steep front of 13 mm. depth, a length of 28 mm., and a breadth of 22 mm., but it is, of course, not so well delimited laterally as in the other directions (forebrain-length 125 mm.).

The rhinocerotid sella space is confluent with the chiasmatic groove; it thus cannot be measured on casts. In Milne-Edwards' sagittal sections of skulls of the Pleistocene *Rhinoceros tichorhinus* and a *R. unicornis*, the sella is deeper and longer (in relation to forebrain length: 161 and 131 mm., respectively) in the larger animal. Prof. W. K. Gregory of New York was so kind as to examine together with the present writer the base of the endocast of the largest known land-mammal, the Oligocene rhinocerotid *Baluchitherium*. This giant had a forebrain only 125 mm. long in its 125 cm. skull. We found the PB ill-defined but apparently large. It seems to have extended over a space of approximately 45 mm. behind the optic foramen; the deepest point of the sella, 5 mm. below the brainbase, is 25 mm. behind the base of the optic foramen. This statement will, of course, become of value only when the PBs of the variously sized living rhinoceroses will have been investigated.

The sella of living horses is known to be extremely shallow; endocasts have no pituitary prominence. No endocast of the little ancestor *Eohippus* is known, and the descriptions of the *Mesohippus* brain neglect the base. When we

compare Trautmann's sagittal sections of the PB of ass and horse, we note a difference significant in the light of the present investigation. The diameters may be said to correspond to the different body-sizes: 17-19 x 16-18 x 4.5 in *Asinus*, and 17-24 x 20 x 6.5-8 in Trautmann's and 21 x 25 x 8.5 in Lothringer's *Equus*-specimens. But *the glandular proportion is much greater in the larger genus*; the pars nervosa is embedded in it like a stone in a fruit, whereas in the smaller genus it really is a posterior lobe, enveloped by the anterior lobe only at its rostral extremity. The same difference in composition is obvious from de Beer's sections of pig and ox PBs ('26); the pars glandularis is far larger in relation to the pars nervosa in the ox than in the pig. This phenomenon is most strikingly illustrated in the whales.

The order Cetacea contains, in the living whale-bone-whales, the largest animals of all times. The reader who has followed our exposition so far will therefore learn without surprise that the cetacean PB is very markedly different from all other mammalian PBs in gross as well as microscopical anatomy. Rather will he be amazed at statements such as: "The underlying significance of the differences . . . remains obscure"; the suggestion that the pituitary modification meets needs of marine life; and the construction of a genetic linkage between those peculiarities of the PB in whales and the loss of their pelvic extremities—all published in the last decade.

The pituitary depression in the cetacean sphenoid is shallow in extant forms, and transverse processes are either hardly perceptible or else absent. Hence the pituitary region of endocasts of living whales is either smooth or shows a slight indistinct prominence. But on endocasts of the earliest whales one finds, apparently as one more trace of their carnivore parentage, an oval prominence at the site of the PB—in the Middle Eocene *Prozeuglodon* as well as in the Upper Eocene *Zeuglodon* (Dart; no measurements). In the Miocene *Prosqualodon*, the pituitary region of the brain case is flat.

The peculiarities of the cetacean PB are: the absence of a pars intermedia and of a residual lumen, and the *great size of the extremely vascular glandular lobe* which is completely separated by a dural fold from the small avascular neural lobe.

The total weight of the whale PB naturally is very small indeed if expressed in percentage of body-volume: 0.0027-0.0034 (man: ♂, 0.010; ♀, 0.014). But Valsö weighed anterior and posterior

lobes of several *Balaenoptera sibbaldi* separately; maximum, minimum and medium numbers are 53.3-16.7-32.5 and 1.9-1.0-1.4 g., respectively. From these numbers the present writer has calculated the ratio of neural lobe to glandular lobe, as: maximum, 1:28; minimum, 1:16.7; medium 1:23. The last-named (medium) proportion also results from Wislocki and Geiling's weights found in a *Physeler* of 45,000 kg. body-weight: pars posterior, 0.55; pars anterior, 12.7 g. (1:23), and likewise from their *Balaenoptera physalus* weights: 1.4 and 32.5 (1:23). Great though the variability in these weights is, *no such ratio is found in any other PB investigated*. From values compiled by Wislocki and Geiling, and van Dyke, the following ratios were calculated for comparison: man: ♂, 1:3.0-3.3, ♀, 1:4.5-4.8; cat: ♂, 1:2.2, ♀, 1:1.8; rabbit: ♂, 1:3.6, ♀, 1:5.1; rat: ♂, 1:4.5-7.5, ♀, 1:5.7-12.2.

If Geiling and Robbins' dorsal views of the intact PB of adult specimens of five cetacean genera (*The Pituitary Gland*) are viewed from our present standpoint, they at once show that the peak of size discrepancy between the two pituitary lobes is reached in the largest genera. Each figure shows the neural lobe lying on a glandular lobe of similar contours like a small object on a large cushion. But the transverse diameters of the neural and glandular lobes, as taken from the figures, are:

Denticeti:

Tursiops truncatus (maximum body-length: 4 m.): 6 and 10 mm. = 1:1.7

Delphinapterus leucas (6 m.): 11 and 23 mm. = 1:2.1

Physeler macrocephalus (23 m.): 3.5 and 21.5 mm. = 1:6.1

Mysticeti:

Balaenoptera physalus (24 m.): 7.5 and 24 mm. = 1:3.2.

Second specimen: 8.5 and 26 mm. = 1:3.1

Balaenoptera sibbaldi (31 m.): 7.5 and 35 mm. = 1:4.7.

These proportions of transverse diameters are not, of course, the proportions of lobe volumes, the discrepancy of which is far greater. In a side view of a *Physeler* PB, the neural lobe is seen as a thin tongue lying on the huge ball of the glandular lobe. But even the diameters show that the characteristic described as particularly *striking* and *obscure*, namely the relative size of the growth-promoting lobe, is the *more striking* within each suborder, the larger the body-size attained in the species, and

therefore *not obscure*. The phenomenon is, in the writer's opinion, fully explained by the fact that the order in which these peculiar PBs occur is the order in which the largest animals developed. Judging from the anatomy of the PB in the porpoise, it seems that a group which is prone to develop giant forms may be provided with a relatively large glandular lobe in its smaller representatives too.

The largest known primate was the Pleistocene *Megaladapis* whose skull was over 30 cm. in length—like *Aepyornis*, a native of Madagascar. Unfortunately, an endocast exists only of the upper part of the brain case. The endocranial casts of *Homo primigenius* likewise do not include the PB.

V. THE RELIABILITY OF THE PALAEO-ENDOCRINOLOGICAL CONCLUSIONS

Doubts have been expressed regarding the reliability of the palaeontologists' inference from the size of the pituitary fossae to their contents. They can now be considered resolved by the data given above, at least in so far as the size differences between the fossae of small ancestors and truly gigantic descendants are concerned. The increase in size, relative to brain size, of the latter's pituitary fossae cannot be due to anything but an enlargement of the growth-promoting glandular lobe of the PB.

Certainly the fossa contains, apart from the pars glandularis proper: meninges, vessels, sometimes cartilage, (in mammals) part of the tuber cinereum, sometimes part of the infundibulum which may contain a cavity, two further but smaller epithelial parts, viz., pars intermedia (absent, e.g., in birds and whales) and pars tuberalis (absent in certain lower vertebrates and in sloths), and, always, a pars neuralis. The latter has recently been found to be another gland of internal secretion (van Dyke, II, p. 291); its hormones, however, influence but the movements of the uterus, blood pressure, and diuresis—on experimental removal of the neurophysis alone, no visible function is suspended, and of course the body is not changed. The changes in body build consequent on radical hypophysectomy are, therefore, due to the loss of the pars glandularis.

Outstanding among these changes is the cessation of growth, although about 15 different hormones are ascribed to the gland. Outstanding among the differences between fossil vertebrates, in

the phylogeny of which the increase in fossa hypophyseos volume far surpasses the increase in volume of the rest of the neurocranium, is the difference in body-size.

It is true that differences have been found between the PBs of small and large related living animals which evade palaeontological investigation, namely, different proportion of the lobes within the pituitary compound, and differences in the histological structure of the glandular lobe. No volumetric comparison of PB or fossa would reveal an increasing preponderance of the glandular, growth-promoting lobe such as is observed in a comparison of the PBs in the whales with increasing body-size. The same would, of course, apply to the two pigeon races of 28 and 55 cm. body-length, the PBs of which have been compared by Rost. He found a considerable amount of colloid-filled cysts in the PB of the smaller race which he regards as holding back in the gland hormones not needed in the formation of the smaller body. Rost's following statement recalls our comparative observations on whales:

"Der Vergleich des glandulären Anteils der Hypophyse lässt zunächst einen wesentlichen Unterschied im Hinblick auf ihre Volumina erkennen, welche in einem Verhältnis von etwa Rö:Mö [larger to smaller race] = 3:2 stehen. Dieses Verhältnis ist in Übereinstimmung zu bringen mit dem Unterschiede der Körperdimensionen" (p. 263).

Unfortunately, neither in rabbits, whales, nor pigeons (apparently the only living animals in which so far PBs of small and large representatives have been compared) has the size ratio between PB and brain been investigated. While these comparisons furnish no direct parallels to our results of endocranial cast measurements, the finding of extraordinarily large glandular lobes in the giant whales and pigeons indirectly stresses our assumption that a larger pituitary fossa of a larger animal signifies an enlargement of no other part of the PB than the glandular lobe.

It follows from the various evidences now at hand that Nopcsa was perfectly right when correlating dinosaurs' giantism with their hypertrophic PB. Yet only recently an objection to Nopcsa's theory has been voiced which must be discussed since it comes from the discoverer of the largest reptilian PBs, Janensch. "Die bekannte Hypothese, die die Riesengrösse der Sauropoden mit einer angenommenen Hypertrophie der Hy-

pophyse in Zusammenhang bringt, scheint mir bei zahlenmässiger Prüfung an Wahrscheinlichkeit einzubüssen."

It is true that the biggest of the three contemporaneous sauropods investigated by Janensch did not have the largest fossa, neither absolutely nor in relation to brain-size. But not even Nopcsa would have expected this; even when referring to established ancestry, he qualified his statement of increase in PB volume to "on the whole".

Apart from his specific discovery that the PB of the largest sauropod individual was not the largest in the suborder, Janensch's general reason for doubting Nopcsa is his objection to comparisons of brain volume and PB volume. This he thinks misleading because the brain of the giant sauropods "naturgemäss relativ klein war"—as, let us add, was any part of their relatively tiny head. While we regard it as fortunate to find the growth-promoting organ so near to the brain, the prototypal organ which is least involved in body enlargement, Janensch stresses the importance of comparing PB-volume with body-volume. His above-quoted conclusion rests on the fact that the PB compares to the body: in pigeons, in the proportion of 1:23,000; domestic fowl, 1:110,000; ducks, 1:200,000; but 1:800,000 in *Barosaurus* and 1:1,800,000 in *Brachiosaurus* whose PB thus appears to be small.

To relegate these figures to their right place in our argument, it is hardly necessary to point to the mechanical impossibility of finding room, in the miniature head of a bulky sauropod, for a PB as large in relation to body-size as is provided for in the big skull of a slender bird. It is sufficient to stress the ordinary variability of the volume of the PB, the relations of which are far from being restricted to growth alone. For instance, the ♂/♀ difference in children from birth to five years of age is no less than a PB-weight:body-weight ratio of ♂♂ 1:44994/♀♀ 1:3252 (Lucien). The average weight of the PB in a nulliparous woman is 61.8 centigrams, in primiparae it is 84.7 cg., in multiparae, 106 cg.; the enlargement takes place in the anterior lobe only, does not affect the length of the PB (hemmed in by the sella), but increases the breadth from 14.4 to 17.5 and the height from 5.9 to 8.0 mm. (Erdheim and Stumm, quoted from Wittek). Wittek's examination of 734 cattle showed that while there is a steady increase of pituitary weight with increase of body-weight in both sexes, two 3-year-old bulls of the

same body-weight had PBs of 1.90 and 3.02 g., respectively; two such cows, even 2.6 and 6.2 g., respectively.

It follows that comparison of conditions in related, contemporaneous, single individuals cannot impair a statement which applies to extensive phylogenetic development: namely, that small dinosaurs had relatively small PBs while PB-volume increased, on the whole, in direct proportion to the development of their giantism.

Consequently, it may well be that when the suggestions made in this paper are carried out by neozoologists, the differences in structure and in size relative to the brain between the PBs of small and gigantic genera expected by the palaeozoologist will fail to be found. Such cases are already established; but they only recall the palaeo- and neo-zoologists' different views of the inheritance of "acquired characters": the palaeozoologist firmly believes that he can follow this phenomenon *throughout the ages*, to which the neo-zoologist retorts that it cannot be demonstrated *in our lifetime*.

The difference between the PB of a small ancestral genus and that of its gigantic descendant does indeed not seem to be paralleled in the volume of the PB of *Felis domestica* and *Felis tigris*, our contemporaneous species of one genus on the same evolutionary level. Robb has already denied any difference between the relationship of PB-weight and that of eyeballs, etc., to body-weight, on the ground that there is no difference in the mass of the PB that can be correlated to the size differences attained in two breeds of one and the same living species, the domestic rabbit. In both these cases, the composition of the PB is not known; furthermore, the animals compared differ exclusively by their size. It is, however, not only size by which *Aepyornis* is distinguished from *Mullerornis*, but there is also a progressive increase of, for instance, bone density in the family. Not only because of their size are the sauropods called "dragons". A long evolution led them away from the unspecialized reptilian type and size of their ancestors. The hippopotamus is not just an enlarged pig as the tiger is an enlarged cat; the sperm whale is not an enlarged porpoise but a porpoise further developed in many ways. It remains to be investigated which kind of size differences are always paralleled by definite size differences of the PB.

No external cause can be made responsible for the development of either individual or phylo-

genetic hyperpituitary giantism. Bailiff's experiments have shown that the PB actually is influenced by external agents: microscopic changes and hypersecretion were produced in the glandular but not in the neural lobe by exposure of rats to cold for 9–56 hours. But human as well as animal giants with extraordinarily active PBs have been observed to develop in their normal surroundings. The sudden manifestation of human hyperpituitarism is a pathological phenomenon to the medical profession whose object is present-day man; yet the palaeontologist notes that it is apt to become a hereditary disposition. The occasional occurrence of chickens with ostrich-like feather peculiarities, however, is a mutation for the zoologist (Murphy); PB and thyroid may be supposed to be the primarily affected organs. Likewise, one tadpole of one frog family in Hahn's aquarium grew to double, and three tadpoles grew to $3\frac{1}{2}$ times the size of the others, and they exhibited very marked anterior lobe hyperplasia.

Phylogenetic trend towards giantism also developed in every kind of environment, through such still unexplained changes in the germ plasm. Its occurrence can all the less be interpreted in terms of Lamarckism since the accompanying bone changes vary from retardation of epiphysis ossification with increased massiveness of the long bones (sauropod dinosaurs) to an abundance of bony outgrowths of the skull (ceratopsid dinosaurs, giant titanotheres, and rhinoceroses) and osteosclerosis (whales). This recalls the different response of different animals to experimental hyperpituitarism.

Whichever conditions may one day be found to start and pave the way for the formation of giant animals, the fact can to-day be considered established, by the palaeontological evidence described above, that phylogenetic evolution of definitely gigantic types is accompanied by a conspicuous enlargement of the anterior pituitary lobe.

VI. SUMMARY

Clinical experience shows that in human giants the glandular lobe of the pituitary body is abnormally enlarged. Experimental administration of glandular lobe extracts stimulates body-growth to such an extent that the animals may grow beyond the maximum normal size of their species. The present investigation furnishes some parallels in natural evolution: phylogenetic development of

giantism in reptiles, birds, and mammals was found to be accompanied by a striking enlargement of the pituitary fossa which can only be due to an enlargement of the glandular lobe which secreted the growth hormone.

In giant Jurassic dinosaurs, the volume of the fossa hypophyseos may amount to 10 per cent of the brain-case volume.

Among the subfossil aepyornithids, pituitary volume compares to forebrain volume as 1:102 in the ancestral genus *Mullerornis* (body-height:148 cm.); within the genus *Aepyornis*, the ratio rises from 1:82 in *A. hildebrandti* (160 cm.) to 1:36 in *A. medius* (211 cm.), and to 1:24 in *A. maximus* (221–300 cm.). While body-height was about doubled, the volume of the forebrain increased by four fifths, but PB-volume became eightfold. The extraordinary size of the aepyornithid eggs and the loose luxuriant plumage of the large ratites now appear as signs of hyperpituitarism.

Similar hypophyseal development as in the aepyornithids is observed in the dinornithids. The small dinornithid *Anomalapteryx* had a relatively larger PB than the larger ostrich; the same was the case in the aepyornithid of ostrich size, and the composition of the porpoise PB points in the same direction: phyla apt to develop giant forms may be provided with a proportionately large glandular lobe also in the smaller representatives. The extraordinary size of the cetacean, particularly of the giant whales' anterior lobe is unparalleled.

Although the sirenian skull usually possesses no pituitary groove, the PB of the 10 m.-long subfossil *Rhytina* left an extensive impression in the sphenoid bone. A comparison of a large series of mammalian endocasts has shown that the PB of giant forms may model the skull base in orders which possess no sella.

The present report is mainly based on endocranial casts, mostly of single representatives of the species. Its significance remains to be tested, as far as this is possible within the extant animal world, by comparative investigation of pituitary glands.

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LIST OF LITERATURE

- BAILLIF, R. N. Microscopic changes in the hypophysis of the albino rat following exposure to cold and their relationship to the physiology of secretion. *Amer. Jour. Anat.*, 62, 475-495, 1938.
- BAUER, J. Hypophyse und Wachstum. *Klin. Wnschr.*, 9, 625-628, 1930.
- DE BEER, G. R. The comparative anatomy, histology and development of the pituitary body. *Biol. Monogr.*, 6, I-XIX, 1-108, 1926.
- . The development of the skull of the shrew. *Phil. Trans. Roy. Soc. London (B)*, 217, 411-480, 1929.
- BENEDICT, E. B., T. J. PUTNAM, and H. M. TEEL. Early changes produced in dogs by the injections of a sterile active extract from the anterior lobe of the hypophysis. *Amer. Jour. Med. Sci.*, 179, 489-497, 1930.
- BROWN, B., and E. M. SCHLAIKJER. The structure and relationships of *Protoceratops*. *Ann. New York Acad. Sci.*, 40, 133-266, 1940.
- CAVE, A. J. E. The craniopharyngeal canal in man and anthropoids. *Jour. Anat.*, 65, 363-367, 1931.
- DEXLER, H. Zur Anatomie des Zentralnervensystems von *Elephas indicus*. Arb. neurol. Inst. Wiener Univ., Festschrift Obersteiner, 1907. (Quoted from notes.)
- VAN DYKE, H. B. The Physiology and Pharmacology of the Pituitary Body. *Chicago*. I: 1936. II: 1939.
- EDINGER, T. Die fossilen Gehirne. *Berlin*, 1929, and: *Erg. Anat.*, 28, 1-249, 1929. (Cf. Bibliography.)
- . Palaeoneurologie. *Fortschr. Palaeont.*, 1, 235-251, 1937. (Cf. Bibliography.)
- , and C. WIMAN. Le crâne et l'encéphale des Aepyornithes. *Mém. acad. malgache* (Not yet printed).
- EVANS, H. M. *et al.* The growth- and gonad-stimulating hormones of the anterior hypophysis. *Mem. Univ. Calif.*, 11, 1-446, 1933.
- FRAAS, E. Die Ichthyosaurier der süddeutschen Trias- und Jura-Ablagerungen. *Tübingen*, 1891.
- FUGO, N. W. Effects of hypophysectomy in the chick embryo. *Jour. Exper. Zool.*, 85, 271-297, 1940.
- GUTOWSKA, M. S. Effects of prolonged oral administration of large doses of pituitary anterior lobe to laying hens. *Quart. Jour. Exp. Physiol.*, 21, 197-216, 1932.
- HAHN, A. Einige Beobachtungen an Riesenlarven von *Rana esculenta*. *Arch. mikr. Anat.*, 80, 1-38, 1912.
- HANDELSMAN, M. B., and E. F. GORDON. Growth and bone changes in rats injected with anterior pituitary extract. *Jour. Pharmac. Exp. Therap.*, 38, 349-362, 1930.
- HENDERSON, W. R. Sexual dysfunction in adenomas of the pituitary body. *Endocrinology*, 15, 111-127, 1931.
- HERRICK, C. J. The amphibian forebrain. I. *Jour. Compar. Neurol.*, 37, 361-371, 1924.
- HILL, R. T. *et al.* Hypophysectomy of birds. *Proc. Roy. Soc. London (B)*, 115, 402-409, 116, 208-236, 1934.
- JAEKEL, O. Epiphyse und Hypophyse. *Sitz. ber. Ges. naturf. Freunde Berlin*, 1903, 27-58.
- JANENSCH, W. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguruschichten Deutsch-Ostafrikas. *Palaeontographica, Suppl.* 7, 1. Reihe, Teil 2, 247-297, 1935.
- KADANOFF, D. Über die Beziehung zwischen der Grösse der Sella turcica und der Schädelgrösse. *Anat. Anz.*, 87, 321-333, 1938-39.
- KEITH, A. An inquiry into the nature of the skeletal changes in acromegaly. *Trans. London Med. Soc.*, 34, 90-119, 1911.
- . The evolution of human races in the light of the hormone theory. *Bull. John Hopkins Hosp. Baltimore*, 33, 155-159, 1911.
- KÜENZI, W. Versuch einer systematischen Morphologie des Gehirns der Vögel. *Rev. Suisse Zool.*, 26, 17-111, 1918.
- LAMBRECHT, K. Handbuch der Palaeornithologie. *Berlin*, 1933. (Cf. Bibliography.)
- LARGER, R. Théorie de la contre-évolution ou dégénérescence par l'hérédité pathologique. *Paris*, 1917.
- LOTHRINGER, S. Untersuchungen an der Hypophyse einiger Säugetiere und des Menschen. *Arch. mikr. Anat.*, 28, 257-292, 1886.
- LUCIEN, M. Les poids, les dimensions et la forme générale de l'hypophyse humaine aux différents âges de la vie. *C.r. Assoc. anat.*, 13, 147-158, 1911 (Quoted from COVELL, *Amer. Jour. Anat.*, 38, 1927.)
- MORTIMER, H. Pituitary and associated hormone factors in cranial growth and differentiation in the white rat: a roentgenological study. *Radiology*, 28, 5-39, 1937.
- MURPHY, R. C. Discussion (of: W. K. Gregory: Origin of ratites and penguins). *Proc. Linn. Soc., New York*, 45-46, 11-17, 1935.

- NOPSICA, F.V. Die Riesenformen unter den Dinosauriern. *Cbl. Min. Geol. Palaeont.*, 332-351, 1917.
- OWEN, R. On Dinornis, Pt. 16. *Trans. Zool. Soc. London*, 7, 381-396, 1872.
- . Memoirs on the extinct wingless birds of New Zealand. *London*, 1879.
- . On Dinornis, Pt. 24. *Trans. Zool. Soc. London*, 11, 257-261, 1883.
- PETERSILIE, Dissertation Jena 1920. (Quoted from DUERST, Grundl. d. Rinderzucht, *Berlin*, 1930.)
- Pituitary Gland, The. An investigation of most recent advances. *Res. Publ. Assoc. Res. in Nerv. and Mental Diseases*, 17, I-XXIV, 1-764, 1938.
- PUTNAM, T. J., E. B. BENEDICT, and H. M. TEEL. Studies in acromegaly. VIII. Experimental canine acromegaly produced by injection of anterior lobe pituitary extract. *Arch. Surgery*, 18, 1708-1736, 1929.
- ROBB, R. C. Is pituitary secretion concerned in the inheritance of body-size? *Proc. Nat. Acad. Sci. Washington*, 14, 394-399, 1928.
- ROMER, A. S. Vertebrate Palaeontology. *Chicago*, 1933.
- ROST, H. Die Entwicklung der Hypophyse der Haustauben und ihre rassetypische Ausbildung bei der Römertaube und der Mövchentaube. *Zeitschr. wiss. Zool.*, 152, 221-276, 1939.
- SMITH, G. E. Catalogue Physiol. Ser. Mus. Roy. Coll. Surgeons, England, 2, Second edition, *London*, 1902.
- STERNBERG, C. M. A new species of horned dinosaur from the Upper Cretaceous of Alberta. *Canada Dept. of Mines, Bull. 54 (Geol. Ser. 49)*, 34-37, 1929.
- STRESEMANN, E. Aves. *Handb. Zool.*, 7, II, 1927-1934.
- TRAUTMANN, A. Die makroskopischen Verhältnisse der Hypophyse einiger Säuger. *Arch. wissenschaft. prakt. Tierheilk.*, 35, 416-437, 1909.
- UHLENHUTH, E. Experimental production of gigantism by feeding the anterior lobe of the hypophysis. *Jour. General Physiol.*, 3, 347-365, 1921.
- VALSÖ, J. Der Hormongehalt der Hypophyse des Blauwals (*Balaenoptera sibbaldi*). *Klin. Wnschr.*, 13, 1819-1820, 1934.
- VERSLUYS, J. Kraniaum und Visceralskelett der Reptilien. *Handb. vergl. Anat. Wirbelt.*, 4, 699-808, 1936.
- VOITKEVIC, A. A. Die morphogenetische Aktivität der verschiedenen Teile der Hypophyse. VIII. Der Einfluss des Hypophysenvorderlappens auf die Schilddrüse und Federbildung bei Tauben. *C. R. acad. sci. URSS*, 17, 157-160, 443-444, 1937.
- WHITE, T. E. On the skull of *Kronosaurus queenslandicus* Longman. *Boston Soc. Nat. Hist., Occ. Papers*, 8, 219-228, 1935.
- . Holotype of *Plesiosaurus longirostris* Blake and the classification of the plesiosaurs. *Jour. Paleont.*, 14, 451-467, 1940.
- WILLISTON, S. W. North American plesiosaurs. *Trinacromerum. Jour. Geol.* 16, 715-736, 1908.
- WISLOCKI, G. B. The hypophysis of the porpoise (*Tursiops truncatus*). *Arch. Surgery*, 18, 1402-1412, 1929.
- . The topography of the hypophysis in the Xenarthra. *Anat. Rec.*, 70, 451-471, 1937-1938.
- . Note on the hypophysis of an adult Indian elephant. *Anat. Rec.*, 74, 321-328, 1939.
- , and E. M. K. GEILING. The anatomy of the hypophysis in whales. *Anat. Rec.*, 66, 17-36, 1936.
- WITTEK, J. Über das Verhalten der Rinderhypophyse bei den verschiedenen Geschlechtern, in der Gravidität und nach der Kastration. *Arch. Anat. Physiol., Anat. Abt., Suppl.* 1913, 127-152.





STRUCTURAL RELATIONS IN CELL RESPIRATION

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INTRODUCTION

THE living cell exhibits two striking and apparently contradictory properties. In the first place, the substances that make up living protoplasm endow it with a certain morphological stability, which expresses itself grossly in the well-known intracellular structures such as the nucleus, chondriosomes, plastids and so on, and more finely in the persistence of the physical and chemical properties of protoplasm through the environmental, developmental, and evolutionary changes to which it is subject. This stability of living organisms, and the relative independence of the cell from alterations in its environmental conditions (within certain limits), was one of the first of its properties to be recognized by biologists and led many to suppose that such effects could only be accounted for by a supernatural and directive "vital force." On the other hand, it was soon made abundantly clear that the apparent stability of the cell and of the whole organism is contingent upon a continuous interchange of matter between the cell and its environment—that life is characterized by the assimilation of substances from the outside world and the concomitant destruction and excretion of intracellular material and of protoplasm itself.

Thus, morphological stability and metabolic activity, while apparently antagonistic, are together the essential properties of all living things. To date it has been impossible to separate these characteristics, and the smallest independent unit of structure, the cell, is also the smallest unit which is capable of maintaining complete metabolic activity. However, in recent years with the development of analytical biochemistry, it has been possible to break down the cell, extract certain of its components, and reproduce *in-vitro* various fragments of the metabolic process. This type of work has accumulated a large body of data which

are in the main limited to the destructive processes alone. Perhaps the best known and most important of these catabolic processes are those involving the oxidative degradation of organic metabolites, which in series make up "cellular respiration."

The very accumulation of these data has, in the last few years, forced upon research workers the problem of integrating this information and relating the separate reactions to the entire respiratory process in the intact cell. It has become generally recognized that the separate *in-vitro* data on the various extracted parts of the respiratory system do not in themselves provide an adequate picture of the behavior of this system in the cell itself. But there is a good deal of disagreement as to the manner in which these analytical data are to be related to the properties of the entire cell.

It has frequently been suggested, for example, that the total living system can be "reconstructed" by fitting together the various reactions which have been studied in extracts, as one would a jig-saw puzzle. Thus, according to D. E. Green (1) the biochemist must "resort to the disorganization of the cell in order to puzzle out the mechanisms of reaction."

The validity of this "reconstruction" method has been severely taxed by the evidence obtained from the extracts themselves. As will be shown below, these *in-vitro* data themselves necessitate the conclusion that the protoplasmic *structure* (which is destroyed in obtaining such data) plays the major rôle in orienting the metabolic reactions within the cell. Further, it will be seen that data obtained from intact cells often disagree with the behavior of reconstituted enzyme systems *in-vitro*.

On the other hand, a number of workers have suggested, on the basis of specific evidence, that the properties of cellular metabolic systems must

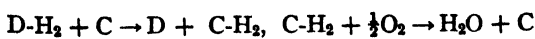
be strongly conditioned by the intracellular structure. Thus Warburg's earliest work on cell respiration was accompanied by a strong emphasis of the rôle played by the structural arrangements of the cell constituents (2). Batelli and Stern (3) spoke of two types of cell respiration, one related to the cell structure and the other to the "fluid" constituents. More recently, Korr (4) finds that "bioluminescence, like many other bacterial oxidative phenomena, is closely associated with cellular structure." Similarly, Stier and Newton (5) conclude that changes in the endogenous metabolism of yeast are related to reorganization of the intracellular structure. Much of this type of implicit evidence has been discussed by Korr (6).

It is becoming increasingly clear that cell structure plays a major rôle in the orientation of cellular metabolic systems, particularly those concerned with oxidations. The literature contains much evidence obtained from intact cells that points to this conclusion. In addition there is a store of information concerning the properties of respiratory enzyme systems which have been extracted from the cell, and so freed from some of its structural limitations. It is our aim to correlate these two types of data with the purpose of describing what may be called the history or development of the structural properties of respiratory enzymes as they pass from the more "chemical" state of the *in-vitro* extract to their biological position in the intact living cell. It is hoped that such a discussion will provide at least a tentative indication of the structural orientations which appear to regulate the activity of cellular enzyme systems.

It is our purpose here to review certain of the data concerning the respiratory properties of both reconstructed systems and intact cells, with the view of demonstrating the relationship between these properties and the internal structure of the cell.

THE SEQUENTIAL NATURE OF THE RESPIRATORY PROCESSES

The net result of aerobic respiration in the cell is the combustion of an organic metabolite, the production of carbon-dioxide and water, and the consumption of oxygen. This process involves a series of oxido-reductions which can be very generally represented thus:



where $D-H_2$ represents the metabolite, D the ox-

idation products of the metabolite (eg. CO_2), C a reversibly oxidizable carrier in its oxidized state, and $C-H_2$ the carrier in its reduced state. Actually, the "carrier" (C) may be a long series of reversible oxido-reduction reactions. The result of this series of reactions is the transference of electrons, but as can be seen above, it is convenient to picture the process in terms of hydrogen transfer.

According to the "reconstruction" technique it is customary to interpret such a serial process in terms of the oxidation-reduction potentials of the individual reactions which constitute the chain. Thus, the generalized system above would be written:

- 1) $D-H_2 \rightleftharpoons D + 2H + 2e$
- 2) $C-H_2 \rightleftharpoons C + 2H + 2e$
- 3) $H_2O \rightleftharpoons \frac{1}{2}O_2 + 2H + 2e$

The tendency of each of these reversible reactions to proceed in one direction or the other is expressed by the electron pressure which they produce or absorb, that is, by the oxidation-reduction potential (E_0). It is then postulated that the ordering of the entire sequence is due to the quantitative relations of the various reaction potentials involved. Thus in the case above, $E_0(3) > E_0(2) > E_0(1)$, and the sequence is thereby determined. It would follow from such an interpretation that the configuration of a chain of respiratory reactions depends on the relations of the E_0 's of the various reversible oxido-reduction systems present in the cell.

The last conclusion is often put forward by adherents of the reconstruction school, although its limitations when applied to *cellular* conditions are also pointed out. However, a further examination of the data reveals that such reconstructed systems are more than merely limited in their application to the living cell. The *in-vitro* data themselves show that the most important factor controlling the ordering of the respiratory systems is the protoplasmic structure which is always destroyed in the course of such experiments.

It is clear that the oxidation-reduction potential indicates merely a *tendency* to react in a particular way. But actual reaction between processes (1) and (2), for example, does not follow from a relation of *tendencies*. In order that the electron transfer really occur, it is necessary that a molecule of $D-H_2$ collide with a molecule of C. That is, the ordering of the series $1 \rightarrow 2 \rightarrow 3$, depends on actual material contact between the reacting substances. The E_0 value of each oxidation-re-

duction equilibrium indicates which reactions are thermodynamically *possible*, but only those *will* occur which are also made possible by molecular collisions.

This requirement at once introduces, in a sense, the importance of structural relations. Even in a homogeneous system, say where substances A and B are dissolved in an inert solvent and $A + B \rightarrow C$, there is an element of "structure". This system is homogeneous if molecules of A and B are free to move about the medium in all directions. However, the occurrence of the chemical change ($\rightarrow C$) depends on the momentary loss of this directional freedom by a molecule of A and of B, that is, the reaction occurs only on *collision*. At the instant of collision, molecules A and B have a fixed spatial relation relative to each other and this relation results in the change to C or in their separation. The homogeneity of this system resides in the fact that the reacting molecules have three degrees of translational freedom, and that their rate of collision is therefore determined by a probability function which is directly proportional to the product of their concentrations. Yet the chemical process itself depends on a spatial or "structural" orientation of A and B, however transitory this moment of collision may be.

THE STRUCTURAL IMPLICATIONS OF HETEROGENEITY

In the case of reactions which occur in heterogeneous systems, such as obtain in the living cell (or in fact in cell extracts as well), the structural orientation, which in the homogeneous system is so transitory, becomes of the first importance.

To return to the generalized diagram of the respiratory process, it must now be pointed out that each step is mediated by a protein enzyme or by a carrier which is linked to a protein. Thus the process: $D-H_2 + C \rightarrow D + C-H_2$ depends on the activation of the H atoms of the metabolite ($D-H_2$) by a *dehydrogenase* enzyme. Similarly the reaction $C-H_2 + \frac{1}{2}O_2 \rightarrow C + H_2O$ depends on the activation of the molecular oxygen by the *oxidase* enzyme.

In fact every reaction that makes up the chain of respiratory processes involves one or more enzymes, and these reactions cannot proceed at any appreciable rate *in-vitro* in the absence of the enzymes. It is hardly necessary to point out how important this enzyme mediation is, except to recall that by this means are produced rapid chemical changes which would otherwise require extremely drastic conditions of temperature, pressure, and pH.

Every known respiratory enzyme (and every other enzyme) including those which have been successfully extracted and purified is at least in part protein. Usually there is associated with the protein a so-called prosthetic group which may be an organic compound containing a heavy metal (usually Fe or Cu) or a reversibly oxidizable dye. Many of the prosthetic groups and certain of the protein bases have been isolated and crystallized. Some of the prosthetic-group-protein compounds appear to be rather loosely bound, but in every case a specific protein is essential to the enzyme activity.

Solutions of such proteins have often been termed "micro-heterogeneous systems". This description is quite apt, in that the protein molecules while dispersed in the solution are so large, as compared to the substrate molecules, that they behave as though in a solid state. Here the spatial relations of the enzyme and substrate become of prime importance.

It is generally accepted that enzyme catalysis involves the formation of a substrate-enzyme complex. Since the enzyme particle is much larger than the substrate molecule (except in the case of extracellular proteolytic enzymes which act on entire protein molecules), this union occurs as a binding of the substrate molecules on the surface of the enzyme. Haldane (7) has calculated that an enzyme of molecular weight 60,000 and density 1.1 would have a surface of 9856 square Ångstroms and could probably hold about 150 hexose molecules. In order to undergo chemical change the substrate must be bound on the enzyme surface, but not all of the surface is catalytically active. Rather, in many cases, it has been found that the activity is restricted to a limited number of surface points. Thus, if saccharase or lipase is adsorbed on an inert substance such as alumina, the enzymatic activity is retained. On the other hand, if lipase is adsorbed on a fat, it loses its enzymatic activity. Thus, it appears that the active centers of the enzyme take part in the binding of its specific substrate.

Similarly, Quastel (8) has shown that the various metabolites which can be oxidized by bacteria are activated by specific dehydrogenases which are characterized by specific "active spots". In general it has been found that dehydrogenases exhibit a high degree of substrate specificity which appears to be dependent upon the presence of specific side-chains on the substrate molecule. In some

cases, enzymes exhibit a stereochemical specificity, as for example the d- and l-deaminases (Krebs (9)).

It becomes clear, therefore, that enzyme catalysis, even *in vitro*, depends on the spatial orientation of the enzyme and its substrate. Not only is it required that the substrate be bound at a specific spot on the enzyme surface, but its link to the enzyme also depends on the presence (on the substrate molecule) of a particular side-chain.

Here, then, the structural factor becomes strongly emphasized. In a homogeneous system the reacting particles have complete freedom of motion, except at the instant of collision. In a micro-heterogeneous enzyme system, the substrate molecules are still free to move about in solution. However, the enzyme is now in effect a two dimensional surface upon which the substrate molecules must become structurally oriented before undergoing any change. In such a system the substrate constitutes one reactant, and the *active-spots* of the enzyme the other reactant. Since the latter are *fixed* points on the surface of the enzyme particle, they cannot exhibit the statistical kinetic behavior characteristic of the free reactants in a homogeneous system.

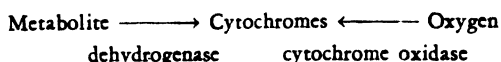
This increase in structural rigidity is reflected in the kinetic properties of heterogeneous enzyme systems. In homogeneous systems the rate of reaction is proportional to the frequency of effective collision and is therefore proportional to the product of the concentrations of the reactants. However, in enzyme systems, while the rate of reaction is still proportional to the number of collisions, that is, to the number of substrate molecules combined with the active spots of the enzyme, the latter value is not always dependent upon the concentration of substrate in the medium. As the substrate concentration is increased from zero, the number of active spots combined with substrate will increase, but this will become limited by the rate of release of substrate molecules in the activated state. Finally, as the rate of collision of active spots with unactivated substrate molecules increases with the substrate concentration, a point will be reached where this rate is equal to the speed of release of the active spots. The rate of substrate activation is now at a maximum, and any further increase in substrate concentration will have no effect on the rate of activation. In this way, the rate of enzyme activity may become independent of the concentration of one of the re-

actants involved. The structural properties of the enzyme thus result in the characteristic relative independence of cellular activity from the outside environment. This phenomenon is characteristic of all enzyme processes, and led Michealis and Menten to the development of the theory of the enzyme-substrate complex.

The intrinsic properties of substances that participate in heterogeneous reactions are also influenced by the structural orientations to which they are subject. Thus, Kuhn and Boulanger (6) find that the E_0 of riboflavin phosphate (the prosthetic group of the yellow respiratory enzyme) is considerably more negative in value than the E_0 of the riboflavin-protein complex. Similarly Korr (11) has demonstrated the shift in E_0 value which occurs when various oxidation reduction systems are bound on surfaces. It must certainly be concluded that the thermodynamic properties of oxidation-reduction reactions become considerably altered when they function within the cell. This places a further limitation on the validity of sequential respiratory systems which are reconstructed from E_0 data obtained from various protein-free oxido-reduction reactions.

On the other hand, if we recognize the significance of the structural properties of the respiratory enzymes, it is possible to find a much stronger basis for the serial ordering of oxido-reductions in the living cell.

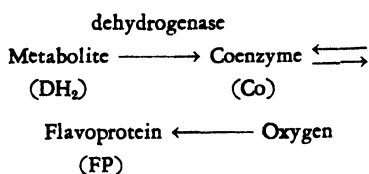
Thus far we have been considering only the relation between an enzyme and a single *substrate*. However, the sequential nature of respiratory enzyme systems makes it necessary for the constituent enzymes really to mediate *two* substrates. This is clearly illustrated in the case of the Warburg-Keilin respiratory system which is responsible for most of the oxidative activity of aerobic cells (for the sake of simplicity various intermediate carriers are omitted):



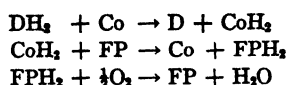
The metabolite is activated by its specific dehydrogenase and is oxidized by reducing the cytochrome (usually by way of the intermediate H transfer via a coenzyme). The reduced cytochrome is reoxidized by molecular oxygen through the mediation of the cytochrome oxidase. The oxygen molecules are bound by the oxidase but at the same time, as Stotz, Altschull and Hogness (12) have recently shown, the cytochrome must also be

combined with the oxidase. Thus, the mediation of the reaction between reduced cytochrome and molecular oxygen requires the simultaneous combination of *both* substances with the oxidase.

A similar relationship is apparent in the yellow enzyme respiratory system:



or:



Here the oxido-reduction reaction between the metabolite and the coenzyme (a reversible oxidizable pyridine nucleotide) is mediated by the dehydrogenase. This enzyme is, of course, a protein and in order to activate the metabolite must first bind it on its surface. In addition, as Warburg (13) has pointed out, the coenzyme must be simultaneously bound by the dehydrogenase protein. Here too, therefore, the transfer of hydrogen occurs only when both reactants are oriented on the surface of the enzyme protein.

The behavior of the flavoprotein is similar. This is an enzyme consisting of an alloxazine-adenine-dinucleotide prosthetic group and a specific protein "base". The prosthetic group is reversibly oxidizable, and its reaction with molecular oxygen depends on the binding of both substances by the protein moiety. Usually the enzyme is thought of as consisting of both the protein and prosthetic group, and only such substances as the metabolite or oxygen given the status of "substrate." Actually, however, both the prosthetic group and oxygen act as substrates of the flavoprotein, while both the coenzyme and metabolite are joint substrates of the dehydrogenase.

It is clear that the ordering of the individual oxido-reductions which make up the cellular respiratory systems is accomplished through the spatial orientation of the various reactants by the appropriate enzymes. Thus, the fact that the metabolite is oxidized by the coenzyme, rather than reacting with some other substance, is due to the joint binding of metabolite and coenzyme by the dehydrogenase. In a similar way the reaction between oxygen and reduced flavin is determined

by the combination of both substances by the same protein. When we further recall that all such combinations must occur at specific points on the protein, it is obvious that the paths of these reactions are determined by the structural properties of the enzyme proteins.

Such *in vitro* systems still retain a certain degree of chemical freedom. The path of the reactions is clearly due to the enforcement by the proteins of a fixed orientation of the various reactants. At only one point in the system is this structural rigidity lacking. This appears in the yellow enzyme system, for example, in the hydrogen transfer by diffusion of the coenzyme between the dehydrogenase and the flavoprotein. This diffusibility, which certainly occurs in such *in-vitro* systems, could permit of certain alterations in the path of reaction—such as reaction of the coenzyme with some other diffusible carrier. However, the main sequential features are determined by the structural properties of the enzymes, and we shall see below that even the small degree of freedom that does occur *in-vitro* is greatly restricted in the cell.

STRUCTURE WITHIN THE LIVING CELL

The foregoing discussion has been restricted to the structural properties of respiratory enzyme systems *in-vitro*. All of the structural restrictions which appear *in-vitro* also hold within the cell, but the normal integrity of the protoplasm must clearly introduce new restrictions which are peculiar to it.

The basis of the relationship between the respiratory activity of the intact cell and the structural properties of the cell protoplasm is, therefore, a problem of the first magnitude. It is, however, unfortunately true that the available data are as yet very inadequate, and any attempt to elucidate the problem must perforce be distinctly tentative.

Three lines of approach suggest themselves: (1) an examination of the chemical behavior of intact cells in order to reveal the nature of the sequential rigidity of the respiratory systems; (2) a study of the effect of natural and induced intracellular structural changes on the characteristics of the respiratory systems; (3) direct observation of the actual molecular architecture of the cell and the description of its relation to changes in enzyme activity. All three approaches are equally important to the solution of the problems of intracellular organization and it may be worth while to examine each of them in greater detail, again using respiration as a general example of enzyme activity.

Structural orientation as expressed in the respiratory activities of intact cells

We have already seen that the chemical properties of the systems discussed above are closely dependent upon the structural orientation of the reactants. Now, if the organizational characteristics of living protoplasm impose new structural restrictions on the chemical processes which it carries out, then some evidence of this should be apparent in the chemical data obtained from intact cells.

That this evidence exists can be seen at once from the fact that the cell's respiratory activity is not carried out by a single system. If all the various oxido-reduction reactions which may take place in the cell were in direct molecular communication one with another, we would then expect the transfer of hydrogen between oxygen and the metabolite, to travel a continuous and uninterrupted path from one reaction to the other. The E_0 values of the various reactions should indicate which linkages are possible, and if this freedom of contact existed, there would automatically be constituted an unbroken chain of H transport, each reaction assuming the place (in the series) dictated by its E_0 value.

In such a (hypothetical) system, the rates of the separate reactions would determine the relative activity of the various branches and shunts in the chain, but the whole sequence would be in a continuous kinetic equilibrium. This indicates a second consequence of such homogeneity: the blocking of one link in the chain (eg. by a poison) should result in the shunting of H transport to other branches of the series, and the reestablishment of equilibrium within the chain. Thus the blocking of O_2 consumption by one part of the system would be expected to result in greater respiratory activity of other parts.

This hypothesis does not meet the test of the *in-vivo* data. The data show that cell respiration is not carried out by a single continuous system. Rather, as we shall see below, the oxido-reduction reactions in the cell have a very restricted course of activity. The various reactions are not in equilibrium with each other, but operate in a strikingly discontinuous manner. The respiratory sequence is not determined by the *possibility* of reaction but by the structural orientation which forces or prevents specific molecular collisions.

An example of this type of evidence is offered by the data on the cyanide-sensitivity of cell respira-

tion (see Commoner (14)). Cyanide, even in maximal concentration, will inhibit only a part of the respiratory activity of most cells. Since cyanide has been shown to be a specific poison for the cytochrome oxidase, this at once indicates that part of the oxygen consumption is not mediated via this enzyme. Further, it can be shown that the cyanide-stable respiration (which is probably due to the activity of a flavo-protein capable of reaction with molecular oxygen) accounts for a small but constant amount of oxygen consumption, while the oxygen utilized via the cyanide-sensitive system is much larger and more variable in magnitude. Changes in respiratory rate which occur during various cytological events such as fertilization of eggs and germination of spores, are accountable by variation in the rate of activity of the cyanide-sensitive system alone. The cyanide-sensitive system appears to use carbohydrates and similar substances, while the insensitive system tends to oxidize proteins and fats. Thus, if glucose is added to a suspension of *Chlorella* cells for example, the rate of oxygen consumption rises sharply, but the amount of cyanide-stable respiration remains constant. If there were a kinetic link between the two systems we would expect the blocking of the cytochrome oxidase by cyanide to result in an increased activity of the insensitive system. In addition it would be expected that the increased respiration due to the addition of substrate would be shared by the two systems. Neither of these effects occur, and it must be concluded that such a kinetic link is lacking. The two systems appear to be distinctly separate mechanisms of oxygen consumption, and it is clear that the constituent oxido-reduction reactions must be rigidly ordered and not subject to free interaction. That this rigidity is a function of the intracellular structure is borne out by the fact that the separation between the two systems disappears when the cellular integrity is disrupted. Thus, Ogston and Green (15, 16) find that the oxidation of hexose phosphate by intact yeast cells is cyanide-sensitive, but its oxidation by a system "reconstructed" from extracts of the same cell is cyanide-stable.

Further evidence of this sort can be found in examining the relationship between respiration and various other cellular functions. Thus, it is found that most changes in respiratory rate during embryogeny occur solely within the cyanide-sensitive system. The variation in respiration between

different species of bacteria and different organs of animals and plants is due to differences in cyanide-sensitive respiration alone. The increased oxygen consumption of muscle and of various glandular tissues incident to their activation, is entirely cyanide-sensitive. Hence, the respiratory dependence of these functions is restricted to a particular part of the total respiratory apparatus of the cell, and again a kinetic equilibrium between the various parts is precluded.

A similar relationship obtains between growth and respiration in plants. Commoner and Thimann (17) have shown that in the *Avena* coleoptile, the effectiveness of auxin as a growth hormone is related to its activation of a specific and small part of the total respiratory system (the four-carbon dicarboxylic acids). The respiratory activity of the four-carbon acids (which are H carriers) is necessary for *all* of growth, but is responsible for but a *small* part of the total respiration; and when it is blocked, growth ceases entirely while the rate of respiration falls but 10 per cent. Again, there is a specific orientation of the component parts of the respiratory system.

Similarly, the data of Fisher (18) and Clowes and Krahle (19) suggest that reproduction of yeast cells is connected with a discrete portion of the cell's respiratory system.

These cases point to the existence of a rigid specificity between the energy producing respiratory processes and the various endothermic functions which utilize the energy thus produced. The energy produced by cellular oxidation cannot be thought of in terms of a pooled fund which is merely apportioned to various endothermic processes according to need. Rather, the union between the two types of process seems to be due to a specific orientation between the two reactions concerned.

The relations of the separate reactions *within* a given respiratory chain seem to follow the same pattern of discontinuity. This has been pointed out for the case of the Warburg-Keilin system by Commoner (14). The activity of the Warburg-Keilin system depends on two *external* factors: the concentrations of molecular oxygen and of the metabolite substrate. The metabolite is activated by its specific dehydrogenase and the rate of dehydrogenation will vary with the metabolite concentration according to the usual hyperbolic function. The same is true of the relationship between pO_2 and oxidase activity, but in this case the

enzyme activity may also be reduced by using greater or lesser amounts of cyanide. Thus, by measuring the rate of respiration of bakers' yeast in various concentrations of dextrose and cyanide it was possible to study the relation between the rate of oxygen consumption and the activity of the oxidase and the dehydrogenase.

If these enzymes were in a kinetic equilibrium we would expect the respiratory rate to be some function of the *product* of the two rates of activity. This, however, does not occur. In low sugar concentrations when the dehydrogenase is relatively inactive, the rate of respiration is not affected by cyanide concentrations which reduce the oxygen consumption of sugar-saturated cells. That is, when the dehydrogenase activity is low, part of the oxidase activity can be negated without affecting the rate of respiration. The inverse relation also holds, for when the oxidase activity is low (in the presence of cyanide), then the rate of respiration is not affected by the addition of dextrose in amounts which would increase the oxygen consumption of unpoisoned cells considerably. This type of kinetic discontinuity has been observed in a number of similar cases (see Commoner (14)).

In the data cited above, we can see a clear reflection of the heterogeneity inherent in the enzymatic catalysis of chemical activities. In the cell itself, the separate reactions that constitute the enormously complicated network of metabolic systems, are rigidly linked in a specific order. The transport of hydrogen is mediated by well-defined and distinctly separate paths, each of which seems to act in a more or less autonomic fashion. The thermodynamic characteristics of the separate reactions are but *permissive* properties; the actual exercise of these potentialities is very limited since the ordering of the respiratory sequence seems to permit few alternative paths of hydrogen transport.

It can be seen that homogeneous kinetic links are almost non-existent in the cellular metabolic apparatus. The separate enzymes, besides having their own internal structural properties, must be held in a fixed orientation relative to each other. There seems to be little or no evidence of homogeneous, "dilute solution" kinetics in the cellular respiratory systems. It must be concluded that the cellular protoplasm is characterized by an inter-enzyme structure which plays the predominant rôle in determining the course of chemical events in the cell.

The effects of changes in intracellular structure on respiratory activity

It is obvious that the mechanical destruction of a cell has a serious effect on its biochemical properties if only because of the fact that disintegration inevitably follows. The effect on respiratory activity is especially marked. Even such a relatively slight mechanical disorientation as mincing has a drastic influence on the respiratory metabolism of most tissues. Intact tissues will deaminate 1-amino acids, but minced tissues will not do so (Krebs(9)). Mincing destroys the capacity of liver tissues to metabolize fatty acids. The mincing of muscle results in a 4- to 6-fold increase in the rate of respiration and a shift of the respiratory quotient from 0.8 to 1.0. That is, mincing brings into play a rapid oxidation of the carbohydrate contained in the muscle (Schorr and Barker (21)). Kostychev has shown that the abrasion of plant tissues increases the rate of respiration and proteolysis. Even the mere bending of a leaf will induce a sharp rise in the rate of respiration (Audas (22)). The literature contains many examples of this kind.

Cytolysis has a similar effect on respiration. The classical work of Warburg (2) although perhaps now overshadowed by his more recent researches is clearly illustrative of this fact. When erythrocytes were cytolysed the rate of respiration fell off sharply. If the cell masses were then centrifuged, the supernatant "structureless" (i.e. liquid) fraction had almost no oxygen consumption while the heavier "structural" precipitate contained all of the respiratory activity of the cytolysate. However, if the latter material was ground up with sand, all of the respiration vanished. Cytolysis of sea-urchin eggs gave similar results, the further significance of which will be discussed below.

That such quantitative effects of cytolysis are based on qualitative disorientation of the respiratory system is apparent in certain more recent researches. Penrose and Quastel (23) found that lysis of *Micrococcus lysodeikticus* results in a 90 per cent reduction in respiration rate. However, while the activity of the dehydrogenases was largely destroyed, the activity of the cytochrome oxidase, catalase and fumarase increased slightly. In some cases, cytolysis increases the rate of respiration, as in amphibian embryos (Brachet (24)), or in the well-known effect of wounding in plant tissues. Specific activities which are related to cell

respiration, such as bacterial luminescence depend on the integrity of the cellular structure (Korr (4)).

It is not surprising therefore, that the characteristics of extracted respiratory systems are often far from similar to those of the system *in-vivo*. Thus, the systematic researches of Ogston and Green (15, 16) on the properties of "reconstructed" enzyme systems reveal that the yellow enzyme system will carry out many oxidations *in-vitro* which it does not mediate in the living cell.

Changes in intracellular structure that occur during the normal life of a cell are also accompanied by such changes in respiratory activity. A case in point is the fertilization of eggs. Almost at the instant at which the sperm penetrates the egg membrane (in the marine eggs at least) a violent churning and streaming begins to agitate the protoplasm, new membranes are elevated from the egg's surface, and embryonic development begins. Such changes must obviously have some effect on the intracellular structure and it is not surprising to find that they are accompanied by sharp changes in respiratory activity. It was first observed by Warburg (25) that fertilization of sea-urchin eggs causes a sudden rise in the rate of respiration. Later investigations by other workers showed that the increase was of the order of 5-7 times, and that it occurred within one minute after fertilization.

Most marine eggs exhibit some change in respiratory rate at fertilization. A summary of these effects by Whitaker (26) shows that the direction of the change of rate depends on the rate of the unfertilized egg. If the respiration of the unfertilized egg is low, then it rises upon fertilization (as in *Arbacia*), but if the absolute rate is at first high, it falls when the egg is fertilized (as in *Chaetopterus*). The absolute rates of various fertilized eggs tend to be very similar in value, fertilization seeming to bring the rate to this general level regardless of its value in the unfertilized egg. It would appear from this that the effect of the activity within the cell at fertilization is to release the unfertilized egg from its stable state by reorienting the enzyme relations in the respiratory system.

That this effect also entails a qualitative change in respiratory activity is shown by the work of Runnstrom (27) and Korr (28) on *Arbacia* eggs. Both demonstrate that the increase in respiratory rate at fertilization is due to the sudden activation of the Warburg-Keilin system. Recently, Balentine (29) has shown that this activation is ac-

complied by an increase in the activity of the dehydrogenases. He has also found that, in the case of *Chaetopterus*, when the rate falls upon fertilization there is a corresponding decrease in dehydrogenase activity.

Later stages in embryogeny show similar respiratory phenomena. Thus, during the diapause in development of Orthoptera, when all developmental activity temporarily halts, the respiration falls to a low value and is completely accountable by a system which is not affected by cyanide. During the active stages in development, however the rate is much higher, and this increase in respiration is due solely to the increased activity of the Warburg-Keilin system. (Bodine and Boell (30)).

Goddard and Smith (31) have shown that the activation and germination of dormant spores of *Neurospora* is accompanied by a forty-fold increase in the rate of respiration. This increase is due to the sudden activation of the Warburg-Keilin system. Similarly the excystment of *Colpoda* from resting cysts, which involves violent intracellular activity and the complete differentiation of the trophic form within one hour after activation, is accompanied by a sharp rise in the rate of respiration (Commoner (32)).

There is little doubt that the structural alteration of the protoplasm produces profound changes in the orientation of the oxidative processes which it mediates. The data cited above but reinforce the conclusion reached on the basis of the sequential properties of the metabolic processes (section 1): The enzymes in the living cell are inter-related in such a manner as to constitute a relatively rigid structure which limits and orients the chemical activities which they carry out.

The next problem which must be faced is the basis of this structural organization.

The molecular basis of intracellular structure

So far, our discussion of intracellular structure has been based on relatively circumstantial evidence. This approach is a necessary and important one, but at the same time must be accompanied by a direct attack on the actual molecular arrangements in the cell and their relation to the chemical rigidity which characterizes respiration in the cell. Very little evidence of this kind is on hand as yet, and the present examination of the problem must perforce be but tentative and suggestive.

The problem of the physical nature of protoplasm has been the subject of extensive research. The older workers, emphasizing the fluidity of protoplasm, have looked upon it as an emulsion of two liquid phases, the one aqueous and the other fatty, with various constituent substances dissolved in each phase. Thus, according to Bayliss (33) "protoplasm behaves as a liquid". On the other hand, the regulated complexity of the chemical behavior of living protoplasm gave rise to a hypothesis of a more rigid cellular structure. This is exemplified in Hofmeister's concept of the cell as a complex of separate "chemical laboratories". In addition the apparent spontaneity and physical autonomy of protoplasmic processes led other workers, such as Pflüger and Verworn to postulate a special kind of living molecule, the biogen, which either constituted the entire cell or served as the "living spark" that activated the "inert" parts of the cell.

Subsequent advance in analytical biochemistry has tended to repudiate this type of concept. Protoplasm was found to contain a huge melange of proteins, carbohydrates, fats, and numerous other kinds of organic and inorganic substances. It seemed absurd to place the burden of protoplasmic "vitality" upon any one of these many constituents.

With the new knowledge that all cellular chemical activities are mediated by enzymes, that all enzymes contain protein moieties, and that the enzymes are structurally inter-related, it is possible, indeed necessary, to re-assess the significance of the protoplasmic constituents. If it is correct to conclude that the organization of metabolic processes and the maintenance of the complicated chemical systems that characterize living protoplasm is accomplished through enzyme inter-relations, then we must look upon the cell's protein constituents in a new light. It would appear that in the proteins can be found the basis of the orientation of metabolic activities, and that the other constituents, however important, must be considered in terms of their relation to the enzymes of the cell. This conclusion is amplified if we further note, that of all cell constituents there is none which possesses the enormous structural potentialities of the long carbon chains and interacting side-chains of the protein molecule. This organizational rôle of the cell protein is borne out by a number of direct experiments.

The early work of Batelli and Stern (3) gave rise

to the concept of two kinds of cell respiration: the "main respiration", which was associated with the intact structure of the cell, and the "accessory respiration" which was a property of the fluid constituents. Warburg (34) found that the granules sedimented (by centrifuging) from ground liver suspension contained 20 per cent of the tissue respiration, while the supernatant fluid contained but 4 per cent. Banga (35) working with pigeon breast muscle suspensions, found that the centrifuged sediment consisted of small granules which contained cytochrome, cytochrome oxidase, succinic, malic, and citric dehydrogenases. However, these granules showed very little oxygen consumption unless the supernatant (which itself had almost no oxygen uptake) was also present. The suspension was therefore presumed to contain soluble coenzymes. More detailed work of this kind carried out by Greville (36) also indicated that both the sediment and supernatant are required for maximum respiration, and it was also shown that in no case did the oxygen consumption persist for longer than some 200 minutes. More recently Stern (37) has shown that the granules (obtained from heart muscle) are apparently spherical macromolecules of a molecular weight of some hundreds of millions. The granules are mainly protein but also contain lipoids, nucleic acid and hemin. Stern also finds the respiratory activity to be of a very short duration.

A similar material has been found by Kabat and Furth (38) and by Claude (39) in a wide variety of normal and malignant tissues. Kabat and Furth have shown that the filterable virus which induces chicken leukemia and sarcoma is associated with a protein particle of the same huge size. Furth and Kabat (40) have also found that the Forssman antigen which occurs in a great variety of species is also associated with this protein fraction in tissue extracts. It is interesting to note that this large protein body often contains as much as 20 per cent of the total N content of cell extracts.

It seems clear that we are here dealing with a very common protein particle which contains a number of enzymes and other active proteins and may carry out, for a short time, oxidative activities in the presence of soluble cell extracts or the proper coenzymes. Stern (41) suggests that this particle contains all the "fixed" enzymes of cell respiration and states: "We consider our particles as 'sub-cellular' functional units and we believe that the active groups of the various component catalysts

are arranged in or on them in an orderly fashion so as to ensure a smooth functioning of the highly complex process of cell respiration." It is also suggested that the respiratory chain is constructed from the enzymes fixed in this particle and the diffusible carriers which link them. (See also Euler and Adler (42), and Dewan and Green (43).)

Do such particles really exist as independent "functional units" within the cell? In the first place it seems clear that these granules, even together with the accessory diffusible coenzymes, do not constitute the entire integrated system of cell respiration, since in no case do such *in-vitro* systems consume oxygen for a period longer than two or three hours. Furthermore, from the evidence cited in the previous sections we must conclude that the relationship between the enzymes "fixed" in the macromolecules, and the carriers which are "freely diffusible" is a rather rigid one. It hardly seems valid to postulate that either part of the respiratory mechanism exists as a structurally free unit within the cell.

The structural rigidity of the position of these macromolecules within the cell is emphasized by the data obtained with the high speed ultra-centrifuge. Particles of such a size should be sedimentable in the ultra centrifuge, but Beams and King (44) find that on the ultra centrifugation of *Ascaris* eggs "No evidence was found which indicates a separation of the ultra-microscopic cytoplasmic components had taken place". Bodine and Boell (45) find that ultra-centrifugation does not affect the rate of respiration of grasshopper eggs in the diapause condition. However, actively developing eggs, which have a much higher normal respiration (which is cyanide-sensitive) suffer a forty per cent reduction in rate. It seems likely that the explanation of this effect and of a similar case in *Arbacia* (Shapiro (48)) is that the large amount of substrate required for the maintenance of high rates of respiration may be in part segregated from the proper enzymes. There does not seem to be any fundamental disorientation of the enzyme system in these cases.

Although the data on this point are still very limited, it seems likely that the enzyme-bearing macromolecules, which can be sedimented *in extracts*, maintain a fixed position when subject to the same gravitational forces *within the cell*. It would seem, then, that this protein, which contains an appreciable amount of the total N in the cell, pervades the entire protoplasm and cannot be

separated from the normal integral structure of the cell. Thus, the enzymes which are associated with this material must also be structurally oriented throughout the cell. Such a structure is reminiscent of the "cytoskeleton" suggested on theoretical grounds by Peters (47) and Needham (48); its relation to cell respiration has been more recently discussed by Korr (6). Such a structure appears to be the organizing medium for the complicated chemistry of cellular metabolism.

It becomes apparent, then, that the enzymes within the cell are under structural restrictions even greater than those characteristic of serial enzyme processes *in-vitro*. Reference above will show that the sequential properties of the yellow enzyme system (for example) *in-vitro* are due to the *internal* structural properties of the two proteins which are involved, both being free to move about in the solution. This freedom, which makes possible the occurrence of oxidative reactions which this system does *not* mediate in the cell is lacking in protoplasm itself.

In the living cell the enzymes seem to be linked together through their mutual association with the heavy protein constituents that pervade the cell. Under these circumstances diffusible hydrogen carriers, such as the coenzymes, appear to be captive within certain parts of the inter-enzyme structure and so serve to further the chemical rigidification of the *in-vivo* respiratory systems. The protein structure within the cell is the organizer of cellular metabolism.

CONCLUSIONS

We have here been concerned with the effect of the structural orientation of cellular oxidative enzymes upon the respiratory activity which they mediate. It seems clear that the ordering of the complex of respiratory processes is dependent on enzyme and inter-enzyme structure.

The importance of this problem is obvious from the breadth of the effects which are included in its scope. The most serious factor limiting the further development of such studies is the need for new experimental approaches and techniques. Three methods of attack were mentioned in the preceding section and it is perhaps appropriate to conclude by suggesting certain new possibilities.

Thus far we have been dealing, in the main, with enzyme systems as already constructed within the cell. In actuality, of course, the respiratory enzyme systems are subject to many developmental

changes. Some of these have been mentioned above as examples of enzymatic reorganizations which accompany structural activations such as fertilization and germination. However, it may also be suggested that such cases of enzyme development may offer opportunities for the study of the structural properties of the respiratory systems which ensue. This could be done, for example, by studying the effect of environmental conditions on the properties of the enzyme systems during the process of development.

Enzyme activation and formation is a very widespread phenomenon and is affected by a number of environmental conditions. Thus Ashford and Dixon (49) show that the K/Ca balance controls the availability of the respiratory enzymes in brain tissue. Similarly Iljin (50) finds that the K, Na/Ca ratio regulates the activity of amylase in leaves. It is possible that this type of effect can be correlated with the known effects of salt balance on protein structure.

What is perhaps a more important influence on enzyme structure is exerted by the substrates themselves. Enzymes can often be produced by introducing the specific substrates to the organism's environment. Such enzyme adaptation or "training" has been found particularly among the bacteria (see the recent review of Dubos (51)). If a bacterium which is normally incapable of oxidizing a particular substrate is cultured in a medium containing this substance, there is often produced, in the course of one or two transfers, the enzyme capable of acting on it. When the substrate is removed the new adaptive enzyme quickly disappears. Thus, the make-up of the respiratory system may be rapidly altered merely by the presence of a new metabolite. Such effects may permit us to study the conditions governing the development of enzyme systems and so to further elucidate their structural organization.

There are, undoubtedly, many such avenues of attack on the relation between cellular metabolism and intracellular structure. There is a clear need for further attention along these lines.

The continued development of our knowledge of cellular respiratory systems, which has in the past been so greatly advanced by analytical biochemistry, now appears to require more than the mere analysis of extracted enzymes. It requires more than the reconstruction of hypothetical systems from the analytical data. In fact, the very accumulation of such data has itself forced

upon us the conclusion that the most important factor determining the course of chemical events in the cell is the very structure which is destroyed in the process of extraction. The old type of analytical biochemistry has itself pointed the way to a new approach.

It is perhaps useful to remind ourselves of

Claude Bernard's characterization of theories: "they are only partial and provisional truths which are necessary to us, as steps upon which we rest, so as to go on with investigation; they embody only the present state of knowledge, and consequently they must change with the growth of science" (52).

LIST OF LITERATURE

- (1) GREEN, D. E. 1937. Reconstruction of the Chemical Events in Living Cells. In *Perspectives in Biochemistry*. (Edited by J. Needham and D. E. Green), pp. 175-186. Cambridge (Cambridge University Press).
- (2) WARBURG, O. 1913. Struktur und chemische Vorgänge im Zelle. Thesis. Heidelberg.
- (3) BATELLI, F., and L. STERN 1907. Action de quelques substances sur l'activité respiratoire des tissus isolés. *Jour. Physiol. Path. gen.*, 9, pp. 228-248.
- (4) KORR, I. M. 1935. The relation between cell integrity and bacterial luminescence. *Biol. Bull.*, 68, 347-354.
- (5) STIER, T. J. B., and M. I. NEWTON 1939. Changes in the rate of respiration of bakers' yeast during assimilation. *Jour. Cell. Comp. Physiol.*, 13, 345-351.
- (6) KORR, I. M. 1939. Oxidation-reductions in heterogeneous systems. *Cold Spring Harbor Symposium*, 7, 74-93.
- (7) HALDANE, J. B. S. 1930. *Enzymes*. London (Longmans, Green and Co.).
- (8) QUASTEL, J. H. 1926. A theory of the mechanism of oxidations and reductions *in vivo*. *Biochem. Jour.*, 20, 166-194.
- (9) KREBS, H. A. 1935. Deamination of amino acids. *Biochem. Jour.*, 29, 1620-1644.
- (10) KUHN, R., and F. BAR 1934. Zum photochemischen Verhalten des Lactoflavins; Modell-Versuche in der Chinoxalin-Reihe. *Ber. Deutsch. Chem. Ges.*, 67, 898-904.
- (11) KORR, I. M. 1938. Oxidation-reduction potentials in heterogeneous systems. *Jour. Cell. Comp. Physiol.*, 11, 233-245.
- (12) STOTZ, E., A. M. ALTSCHUL and T. R. HOGNESS. 1938. The cytochrome C-cytochrome oxidase complex. *Jour. Biol. Chem.*, 124, 745-754.
- (13) WARBURG, O. 1938. Chemische Konstitution von Fermenten. *Ergeb. Enzymf.*, 7, 210-245.
- (14) COMMONER, B. 1940. Cyanide inhibition as a means of elucidating the mechanisms of cellular respiration. *Biol. Rev.*, 15, 168-201.
- (15) OGSTON, F., and D. E. GREEN 1935. The mechanism of the reaction of substrates with molecular oxygen. I. *Biochem. Jour.*, 29, 1983-2004.
- (16) —, and — 1935. The mechanism of the reaction of substrates with molecular oxygen. II. *Biochem. Jour.*, 29, 2005-2012.
- (17) COMMONER, B., and K. V. THIMANN 1941. On the relation between growth and respiration in the *Avena coleoptile*. *Jour. Gen. Physiol.*, 24, 279-296.
- (18) FISHER, K. C. 1940. Urethane and the respiration of yeast cells. *Collecting Net*, 15, 65.
- (19) CLOWES, G. H. A., and M. E. KRAHL 1936. Studies on cell metabolism and cell division. I. On the relation between molecular structures, chemical properties, and biological activities of the nitrophenols. *Jour. Gen. Physiol.*, 20, 145-171.
- (20) COMMONER, B. 1939. The effect of cyanide on the respiration of baker's yeast in various concentrations of dextrose. *J. Cell. and Comp. Physiol.*, 13, 121-138.
- (21) SCHORR, E., and S. B. BARKER 1939. *In vitro* action of insulin on minced avian and mammalian muscle. *Biochem. Jour.*, 33, 1798-1809.
- (22) AUDUS, J. L. 1939. Mechanical stimulation and respiration in the green leaf. II. Investigations on a number of angiospermic species. *New Phytol.*, 38, 284-288.
- (23) PENROSE, M., and J. H. QUASTEL 1930. Cell structure and cell activity. *Proc. Roy. Soc. (B)*, 107, 168-181.
- (24) BRACHET, J. 1934. Étude du métabolisme de l'oeuf de grenouille (*Rana fusca*) au cours du développement. *Arch. de Biol.*, 45, 611-727.
- (25) WARBURG, O. 1908. Beobachtungen über die oxidations Prozesse im Seeigeelei. *Zeit. Physiol. Chem.*, 57, 1-16.
- (26) WHITAKER, D. M. 1933. On the rate of oxygen consumption by fertilized and unfertilized eggs. V. Comparisons and interpretation. *Jour. Gen. Physiol.*, 16, 497-528.
- (27) RUNNSTROM, J. 1930. Atmungmechanismus und Entwicklungserregung bei dem Seeigeelei. *Protoplasma*, 10, 106-173.
- (28) KORR, I. M. 1937. Respiratory mechanisms in the unfertilized and fertilized sea urchin egg. A temperature analysis. *J. Cell and Comp. Physiol.*, 10, 461-485.

- (29) BALLENTINE, R. 1940. Analysis of the changes in respiratory activity accompanying the fertilization of eggs. *J. Cell. Comp. Physiol.*, 15, 217-332.
- (30) BODINE, J. H., and E. J. BOELL 1934. Respiratory mechanisms of normally developing and blocked embryonic cells (Orthoptera). *Jour. Cell. Comp. Physiol.*, 6, 97-113.
- (31) GODDARD, D. R., and P. E. SMITH 1940. Respiratory block in the dormant spores of *Neurospora tetrasperma*. *Plant Physiol.*, 13, 241-264.
- (32) COMMONER, B. 1940. (Unpublished.)
- (33) BAYLISS, W. M. 1927. Principles of General Physiology. Fourth Edition. London (Longmans, Green and Co.).
- (34) WARBURG, O. 1913. Über sauerstoffatmende Körnchen aus Leberzellen und über Sauerstoffatmung in Berkefeld-Filtraten wässriger Leberextrakte. *Pflüger's Arch.*, 154, 599-617.
- (35) BANGA, I. 1937. Über den Aktivator und Donator der Hauptatmung des Taubenbrustmuskels. *Zeit. Physiol. Chem.*, 249, 183-188.
- (36) GREVILLE, G. D. 1937. Fumarate and tissue respiration II: The respiration of pigeon breast muscle dispersions. *Biochem. Jour.*, 31, 2274-2286.
- (37) STERN, K. G. 1940. Biological oxidations and reductions. *Ann. Rev. Biochem.*, 9, 1-42.
- (38) KABAT, E. A., and J. FURTH 1940. Chemical and immunological studies on the agent producing leukosis and sarcoma of fowls. *Jour. Exper. Med.*, 71, 55-70.
- (39) CLAUDE, A. 1937. Fractionation of chicken tumor extracts by high speed centrifugation. *Amer. Jour. Cancer*, 30, 742-748.
- (40) FURTH, J., and E. A. KABAT 1940. Association of the heterogenic antigen with a material in normal and tumor tissues sedimentable at high speeds. *Science*, 91, 483-485.
- (41) STERN, K. G. 1939. Respiratory catalysts in heart muscle. *Cold Spring Harbor Symposium*, 7, 312-322.
- (42) EULER, H. VON, and E. ADLER 1937. Co-Zymase das wasserstoffübertragende Co-Enzym bei der Muskel-Glycolyse. *Zeit. Physiol. Chem.*, 245, 217-245.
- (43) GREEN, D. E., and J. G. DEWAN 1937. The reversible oxidation and reduction of co-enzyme, I. *Biochem. Jour.*, 31, 1069-1073.
- (44) BEAMS, H. W., and R. L. KING 1937. The suppression of cleavage in *Ascaris* eggs by ultracentrifuging. *Biol. Bull.*, 73, 99-111.
- (45) BODINE, J. H., and E. J. BOELL 1936. The effect of ultracentrifuging on the respiratory activity of developing and blocked embryonic cells (Orthoptera). *Jour. Cell. Comp. Physiol.*, 7, 455-463.
- (46) SHAPIRO, H. 1935. The respiration of fragments obtained by centrifuging the egg of the sea urchin, *Arbacia punctulata*. *Jour. Cell. Comp. Physiol.*, 6, 101-116.
- (47) PETERS, H. 1938. Proteins and Cell Organization. In Perspectives in Biochemistry (Edited by J. Needham and D. E. Green), pp. 36-44, Cambridge (Cambridge Univ. Press).
- (48) NEEDHAM, J. 1937. Order and Life. *New Haven* (Yale University Press).
- (49) ASHFORD, C. A., and M. DIXON 1935. The effect of potassium on the glucolysis of brain tissue with reference to the Pasteur effect. *Biochem. Jour.*, 29, 157-168.
- (50) ILJIN, W. S. 1938. Quoted in Oparin, The Origin of Life. *New York* (The Macmillan Co.).
- (51) DUBOS, R. J. 1940. The adaptive production of enzymes by bacteria. *Bact. Rev.*, 4, 1-16.
- (52) BERNARD, CLAUDE. 1865. Introduction à l'étude de la médecine expérimentale, *Paris*.





SUPERNUMERARY MAMMAE, WITH SPECIAL REFERENCE TO THE RHESUS MONKEY

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SUPERNUMERARY breasts have been observed in the human with such frequency that little interest attaches at present to case reports of this condition, unless associated with unusual features. Deaver and McFarland collected 10,895 cases of supernumerary breasts from the literature in 1917 and de Cholnoky (1939) has recently added several more. From this vast material much information of statistical interest has been gained, and together with embryological studies, has helped dispel many of the misconceptions and superstitions which have permeated the subject. Studies of the occurrence of accessory nipples and mammary glands in other mammals have also been of great value in obtaining a truer interpretation of the biological significance of these anomalies. The object of the present paper is to examine the various views which have been held on the many interesting problems connected with the subject, and to report some observations on the occurrence and biological properties of supernumerary nipples and mammary glands in the rhesus monkey.

Interest in accessory mammae is manifested even in the art of the ancients, who occasionally endowed their goddesses with a number of breasts. The Phoenician goddess Astarte, for example, is said to have been frequently represented as having several mammary glands, and the statue of Diana of Ephesus, in the Vatican Museum in Rome, shows an extreme degree of polymastia, symbolic of fertility.

The early references to the subject plainly reveal the complete ignorance which existed concerning the significance of supernumerary breasts. One finds them referred to as *Teufelswerk*, *opus mirabile naturae ludentis*, and *une sorte de caprice ou de bisarrierie* (Hug, 1908). It is even stated (McGillucuddy, 1891) that Anne Boleyn was put to death by Henry VIII because she had a third breast.

ETIOLOGY

Concerning the etiology and mode of formation of supernumerary breasts several theories have been advanced; yet none is entirely capable of explaining all cases of polymastia.

1. Meckel von Hemsbach, in 1852, proposed the view that five was the original normal number of mammary anlagen in the human; of these, one pair being situated in the pectoral region, one pair in the axillae, and the fifth in the midline at the base of the ensiform process. Ordinarily the superfluous glands underwent complete atrophy, but the occasional persistence of one or more of them he regarded as a satisfactory explanation for all the cases of ectopic mammae which came under his scrutiny. There was little if any evidence to support such a theory. It consequently attracted few adherents and soon fell into complete disregard.

2. Ahlfeld (1880) advanced the theory that polymastia was due to a splitting of the mammary anlage during embryonic life, and several years later Hansemann (1889) and Sutton (1889) expressed essentially the same idea. Ahlfeld also invoked the aid of the amnion in accounting for the location of the ectopic glands encountered. Their transplantation to various parts of the body surface was believed to have been brought about through the mechanical action of amniotic pressure and amniotic adhesions. Modern studies by Streeter, however, have demonstrated the inadequacy of amniotic adhesions in explaining the occurrence of various types of congenital abnormalities and have redirected attention from the mechanical action of the membranes to imperfections of the germ plasm.

3. Axillary swellings occur with relative frequency in puerperal women, and when associated with nipples or pores they often secrete a fluid

which is indistinguishable from milk. These tumors have generally been regarded as supernumerary mammary glands, but Champneys (1886), and later Seitz (1909), have regarded them as modified sweat glands which secrete milk under the appropriate hormonal stimulation of pregnancy and lactation.

4. Perhaps the most widely accepted interpretation of polymastia is that which regards this condition as a manifestation of atavism or of reversion. In the human, as well as in all other primates higher than lemurs, only one pair of mammary glands normally occurs. The lemur, however, possesses in addition to the pectoral glands a pair of inguinal "anchoring nipples," for the attachment of the young. Most species of sub-primate mammals possess a greater number of mammary glands, and in the insectivore *Centetes* eleven pairs are normally found.

Charles Darwin, from his study of comparative anatomy, and without the benefit of modern embryologic knowledge, came to the conclusion that polymastia in the human was a manifestation of reversion. In 1868, discussing this condition, he wrote as follows: "Many monstrosities can hardly be considered as the result of an arrest in development; for parts of which no trace can be detected in the embryo, but which occur in other members of the same class of animals or plants occasionally appear, and these may probably with truth be attributed to reversion," and in a later sentence he expresses himself as having been led "to the belief that in all cases the additional mammae in woman are due to reversion." In his *Descent of Man*, however, published several years later (1871), he finds it difficult to explain the occasional occurrence of mammae erratae on the back, thigh, or in the armpit, and admits that "the force of my argument is greatly weakened or perhaps quite destroyed."

A knowledge of the embryonic development of the mammary gland is indispensable to an understanding of more recent interpretations of the significance of polymastia. In the human, as in all other mammalian forms that have been studied, the mammary apparatus is derived from a paired epithelial thickening which runs longitudinally along the ventral surface of the embryo from the anterior to the posterior limb bud, and which is known as the *Milchleiste* (Schultze, 1892) or milk line. Hirschland (1898) has traced this structure even farther back and has found it to be derived in turn from another formation called

the milk streak, which consists of a comparatively broad zone of the integument characterized by higher epithelium and by a condensation of the underlying mesenchyme. During the course of further development, localized elevations appear along the milk line, and the intervening portions disappear. Schultze (1892) has discussed the occurrence of the milk line in several mammalian species, and in addition to the "definitive Zitzen" which persist and represent the mammary anlagen, he mentions the occurrence of "primitive Zitzen" which later disappear. Schmidt (1897) made essentially similar observations on human material and concurred with Schultze in the view that these structures represent supernumerary mammary anlagen. Schultze therefore regarded polymastia as of ontogenetic as well as phylogenetic significance. Schmitt (1898) and Walter (1902), on the other hand, have questioned the interpretation that all such epithelial thickenings represent accessory mammary anlagen. Nonetheless the view as enunciated by Wiedersheim (1908) came to be the generally accepted one, namely, that a condition of hyperthelia normally exists in the human embryo, and that occasionally, in addition to the main mammary anlagen, one or more of the supernumeraries also undergo further development, thereby resulting in postnatal hyperthelia or hypermastia.

Leichtenstern (1878) and Neugebauer (1886) had already expressed their belief that polymastia was a manifestation of atavism, and upon the basis of the detailed embryologic studies mentioned, this view was soon subscribed to by Bonnet (1892), Kayser (1908), Bresslau (1909), and others.

5. Accessory mammary glands or nipples occurring in the vicinity of the primitive milk lines are perhaps adequately explained by the latter theory. Axillary, thoracic, abdominal, inguinal, and possibly vulvar mammae fall into this category. However, the literature contains numerous case reports, apparently well authenticated, of mammae erratae occurring in bizarre locations such as on the face, ear, neck, arm, thigh, and buttock. No satisfactory explanation has been advanced for the development of these ectopic breasts, and they are simply referred to as sports or freaks of nature.

LOCATION, NUMBER, AND INCIDENCE

Although supernumerary mammary glands and nipples have been observed in many atypical posi-

tions (see reviews by Deaver and McFarland, and by de Cholnoky), the vast majority occur along the milk line, from the axilla to the groin, and most of them have been observed in the thoracic region. They may be unilateral or bilateral and may occur above or below the normal mammae. Von Bardeleben (1893) found among 8,568 young men with hyperthelia an incidence of thirty per cent of the supernumeraries occurring on the right side, thirty-nine per cent on the left side, and thirty-one per cent bilaterally. This is in general agreement with the findings of other authors (Leichtenstern, 1878; Bruce, 1879; Iwai, 1907a; Hathaway, 1909; and Landauer, 1939), who found a slight preponderance in favor of the left side.

When the extra nipple is situated above the normal one it is usually lateral to it, whereas when below it is medial. In general, as pointed out by Geoffroy Saint-Hilaire (1832), if a supernumerary gland is situated laterally it is well formed, of considerable size, and can lactate; if medial, it is usually small, imperfectly developed, and incapable of lactation. Most of the above authors have found the majority of the accessory mammae below the normally situated one, and Kajava *et al.* (1921), in their extensive study of a huge Finnish population, found 98.7 per cent of all accessory glands below the normal breasts. Iwai (1907a), however, in his examination of 511 Japanese polymastics, found eighty-eight per cent of the supernumerary breasts above the normal ones, thereby emphasizing the importance of the racial factor. He also found the incidence among females to be three times as great as among males, in contrast to the statistics of Leichtenstern, Bruce, Kajava *et al.*, and Landauer, which indicate a preponderance of supernumeraries among males.

Single accessories occur with the greatest frequency, and the incidence decreases inversely to the number of mammae. Graham-Campbell (1936) has reported the case of a patient with eight and possibly nine supernumerary nipples, and Neugebauer (1886) and Hirst (1912) described patients with eight and seven supernumerary breasts respectively, each of which secreted milk after childbirth.

Great variations exist among the statistical reports concerning the incidence of supernumerary nipples and mammary glands. Kajava *et al.* have reviewed the literature on the subject and have tabulated the incidences quoted by various authors, ranging from 0.05 per cent (Schwalbe) to 23.3 per cent (von Bardeleben). They them-

selves quote an incidence of 2.8 per cent for the Finnish population, as compared with an incidence of 3.75, quoted by Iwai for the Japanese. More recent estimates indicate that the true incidence is probably closer to one per cent. Tiffany (1906) has stated that the condition is more common among Negroes, and Stannus (1914) found fourteen cases among several native African tribes in Nyasaland. Although racial factors undoubtedly play an important rôle in explaining the apparent discrepancies, probably more importance should be attached to the different criteria used by the various observers in making the diagnosis of hyperthelia.

STRUCTURE

Kajava *et al.* (1921) classified supernumerary breasts into eight groups, depending upon the presence or absence of the nipple, areola, hairs, and mammary parenchyma. Twenty-six such breasts were subjected to histologic examination and were found to show all gradations from a structure barely suggestive of mammary tissue to that of a "typical" breast. Hoepfner (1899) had earlier examined nine male accessory nipples histologically and found a normal nipple structure, usually associated with only rudimentary mammary glandular tissue or sweat glands.

HEREDITARY ASPECTS; RELATION TO FECUNDITY AND TWINNING

It has long been realized that throughout the mammalian series the number of mammary glands characteristic of any species is, as a general rule, correlated with the average litter size of that species. This concept has been applied to the subject of polymastia in the human. In addition to its manifestation by the endowment of the goddesses of fertility with supernumerary breasts, the belief has become firmly established in scientific writings that fertility and twinning are associated with the occurrence of polymastia. Leichtenstern (1873) found three cases of twins among seventy patients with accessory mammarys, and Iwai (1907b) reported eighteen cases of multiple birth among 101 married women who had supernumerary glands. Although the total number of pregnancies is not stated, it is certain that the incidence of twinning in this group was larger than in the general population. The latter author also stated his belief that women with supernumerary mammary glands have a tendency to become pregnant

more frequently than others. Numerous case reports tend further to emphasize the relation between polymastia and multiple births. Marie (1893), for example, reported six pairs of twins in two generations of polymastics, and Pétrignani (1939) found six pairs of twins and a set of triplets in three generations of a family possessing this trait.

An experimental basis for this association was apparently established by the breeding experiments of Bell (1923), who succeeded in developing a flock of sheep with four or more nipples, and in which the ewes continued to bear twins or triplets every year, with hardly any single pregnancies. Bell's breeding data were later subjected to genetic analysis by Castle (1924) and by Ritzman (1933) and it was found that there was no necessary relation between nipple number and twinning. Geoffrey Saint-Hilaire (1832) and Flechsig (1840) had long before expressed their disbelief in any relation between polymastia and multiple births or fecundity, and recent writers have been of the opinion that the formerly held views were based upon inadequate statistics. More careful collection and evaluation of statistical data are needed before the problem can be considered settled.

The hereditary nature of supernumerary nipples and mammary glands has been subject to less controversy, for the familial occurrence of these anomalies has been generally recognized. Woodman (1868) reported a case of mother and daughter with third nipples in the same relative positions. Handyside (1873) described bilateral supernumeraries in brothers, and the present writer has found the same condition in father and son. Polymastia has also been reported in identical twins (Weitz, 1925; Birkenfeld, 1932). Cases illustrating the familial nature of supernumerary mammae have been observed with such frequency in recent years that the majority are of insufficient interest to warrant publication. Especially interesting is the report of Klinkerfuss (1924), who traced this condition through four generations of a family. Most famous, however, is the report by Marie (1893), in which is described the occurrence of supernumerary nipples in a young girl, all of her eleven siblings, her father, five paternal uncles, the grandmother, and the paternal great grandmother, a total of twenty cases in four generations.

RELATION TO TUBERCULOSIS

Claims for the association of polymastia with tuberculosis originated with the Japanese. Sato is

said to have found nineteen cases of actual or suspected tuberculosis among twenty-nine individuals with polymastia, and the subject was investigated more extensively by Iwai. The latter author (1906, 1907c) found 4.97 per cent of 1930 tuberculous patients to have supernumerary breasts, as compared with an incidence of 2.71 per cent among 1514 non-tuberculous patients. Conversely, of ninety-six cases of polymastia, he found twenty-three per cent to be tuberculous, as contrasted with a tuberculosis incidence of ten per cent among non-polymastics. On the basis of these figures he maintained that cases of polymastia are found more frequently among the tuberculous, especially those with pulmonary tuberculosis, and that individuals with supernumerary breasts are more liable to be affected by tuberculosis than are others. Boenheim (1919) and Kajava *et al.* (1921) have been unable to confirm these associations among Caucasian races, and the claims of the Japanese authors have not received general acceptance.

RELATION TO LEFT-HANDEDNESS AND TO CONGENITAL ANOMALIES

The interesting observation has recently been made by Landauer (1939) that the incidence of left-handedness is higher among individuals with supernumerary nipples than among the general population. He found 145 of 709 cases of hyperthelia to be left-handed (twenty per cent), as compared with an incidence of eight per cent for this trait among the population at large. Stier (1912) had previously claimed that in left-handed individuals supernumerary areolae occur practically always on the left side, as contrasted with a right sided preponderance of supernumeraries among right-handed individuals.

Boenheim (1919) studied forty-eight cases of supernumerary nipples for manifestations of other anomalies and succeeded in demonstrating a high incidence of coincident abnormalities of various types. Malformations of the ears, he stated, were seldom absent, and skin anomalies (chloasmae, naevi, etc.) were common. Other coincident pathologic conditions which he recorded included imperfections of the eye (Horner's syndrome, abnormalities of the iris), high palate, various anomalies of the chin and teeth, gastric an- or hypo-acidity, *Tropfenherz*, epigastric hernias, and split ensiform processes.

CLINICAL ASPECTS

Supernumerary breasts are of interest chiefly from an academic standpoint. Nonetheless there are several conditions which demand consideration by the clinician. Perhaps the most common source of annoyance from accessory mammae is the pain which they cause during lactation. This is especially so if the gland is not equipped with an adequate outlet for its secretions. If a nipple and ducts are present, the dribbling of milk which frequently occurs may be quite bothersome to the patient. Cosmetic considerations are responsible for the formidable concern which many individuals manifest for the presence of supernumerary breasts, especially if they are large or if they occur in conspicuous or embarrassing locations such as the face, neck, buttock, labia, etc.

Von Bardeleben (1891) suggested that accessory nipples and mammary glands are more prone to pathologic changes than are normal ones, and Williams (1895) reported a high incidence of neoplastic disease (fibroadenoma and carcinoma) in ectopic mammary tissue. Deaver and McFarland (1917) analyzed the reported cases of tumors arising in supernumerary breasts, and de Cholnoky (1939) mentions several more. Yet it is by no means established that tumors arise with greater frequency in ectopic mammary glands than in normally situated ones.

POLYTHELIA AND POLYMASTIA IN SUB-HUMAN PRIMATES

In contrast to the voluminous literature relating to supernumerary mammae in the human, there is a surprising paucity of information concerning their occurrence in many lower forms, and the writer has been able to find only eight reports of supernumerary nipples in sub-human primates.

Sutton (1889) reported two cases in monkeys (a female *Macacus sinicus* and a male *Cercopithecus palas*), both accessories being on the left side, about one inch below the normal nipple. Schickele (1899) found a case of hyperthelia (in *Macacus cynomolgus*) among twenty-eight old world monkeys and five cases among twenty-two platyrrhines of various species, all the supernumerary nipples occurring below the normal ones. Each of these animals had an extra nipple on the left side, and in three the accessories occurred bilaterally, one of them (*Cebus hypoleucus*) having two pairs. Two years later Beddard (1901) exhibited the skin of a female monkey (*Cercopithecus*

schmidtii) which possessed a pair of additional mammae below the normal pair, and the right supernumerary was said to be fully as large as the normal one. Zuckerman (1935) found an extra nipple (right side, below the normal gland) in a pig-tailed macaque (*Macacus nemestrinus*), and three cases of supernumeraries in baboons (*Papio porcarius*). In one animal the accessories were bilateral. An instance of hyperthelia has also been reported (Owen, 1868) in an orang-utan (*Pithecus satyrus*), the accessory nipple occurring on the left



FIG. 1. MONKEY NO. 118. TYPICAL SUPERNUMERARY NIPPLE, BELOW RIGHT NORMAL NIPPLE

side below the normal one. Coolidge (1933) found a case of bilateral supernumerary nipples, occurring below the normal ones, in a chimpanzee. This was the only case that was observed among over 600 hides of great apes that he examined. (In a report now in preparation, which the present writer has very kindly been allowed to read in preliminary draft, H. J. Coolidge, Jr. will describe an additional case of hyperthelia in a chimpanzee, as well as, for the first time, supernumerary nipples in a Siamang and a Gibbon.) Elder (1936) added an interesting case of bilateral

hyperthelia (below the normal nipples) in a female chimpanzee, which gave birth to a male offspring which showed the same distribution of accessory nipples as the mother. This case is of additional interest in that the mother was the half-sister of twins.

Only two cases have been reported of supernumerary nipples in the rhesus monkey (*Macaca mulatta*). Hartman (1927) described the first in a mature female, and Zuckerman (1935) reported a case in a young male. In both instances the extra nipple was on the left side, below the normal one.

mammæ have been observed, in addition to the case previously published by Dr. Hartman.

Approximately one thousand rhesus monkeys have passed under scrutiny in the Carnegie and associated laboratories. Thus, the incidence of this condition is about 1.4 per cent, or within the same range as the most reliable estimates for the human. All occurred in the thoracic region, along the approximate course of the embryonic milk line. In eleven cases the supernumerary was unilateral, and in two cases bilateral and symmetrical. Of the unilateral accessories, six occurred on the left side



FIG. 2. MONKEY NO. 593. SUPERNUMERARY AREOLA, BELOW LEFT NORMAL NIPPLE

Personal observations

While a guest at the Embryological Laboratory of the Carnegie Institution in Baltimore, the writer was extended the opportunity of studying the huge collection of rhesus mammary glands which had been acquired by Dr. Carl Hartman over a period of years, as well as the breasts of the intact macaques which comprise the large Carnegie colony at present. Dr. Hartman has long been interested in the subject of polymastia and has, in addition, collected pertinent notes and photographs which he very kindly placed at the writer's disposal. In all, thirteen cases of supernumerary

and five on the right. All were below the normal breast. This again agrees well with most statistics concerning the incidence of distribution in the human. Twelve of the thirteen cases were females, but this figure is of little significance, since the vast majority of the monkeys in the colony have been females.

In most instances the supernumerary nipple was distinctly smaller than the normal one. Fig. 1 shows a typical example. All gradations in size were observed, however, from a bare accessory areola (Fig. 2) to a supernumerary nipple which was indistinguishable from the normal one.

The accessory breasts were removed, either at operation or at autopsy, in one piece with the ipsilateral normal breast. The nipples were sectioned longitudinally and studied microscopically. The surface epithelium was often found to be thinner in the accessory nipples than in the normal ones. Otherwise, little histologic difference between the two was detected. The underlying fascia was dissected under the binocular microscope, to determine the presence or absence of mammary parenchyma in connection with the supernumerary nipple. In only 5 instances was there any accessory glandular tissue present, and this usually consisted of only a few short ducts radiating from the base of the nipple. There was no continuity between the normal and supernumerary mammary glands. Fig. 3 shows a mount of a typical supernumerary gland, consisting of two short ducts, and indicates its relation to the lower border of the ipsilateral normal gland.

No definite statement can be made concerning the hereditary aspects of polythelia or its possible relation to multiple births in the rhesus monkey. Two animals warrant brief mention, however, because of the strong probability that they were twins, or at least sisters. Monkeys nos. 272 and 273 arrived together in the same shipment from an animal dealer in New York City. They possessed bilateral supernumerary nipples and appeared so similar in all other respects that the animal keepers, who can ordinarily tell the monkeys in the colony apart with little difficulty, were unable to distinguish between them. Although actual proof is lacking, the presumption is strong that they had a common parentage.

In Zuckerman's report (1935) mention is made of the increase in the prominence and color of a supernumerary nipple of a male rhesus monkey following injections with estrin. This demonstrated the responsiveness of the structure to estrogenic hormone. It has recently been shown (Lamar and Speert) that the macaque nipple responds in a striking manner to the local application of an alcoholic solution of estrogen, when the nipple is painted daily with the hormone. This type of treatment was applied to the accessory nipples of 2 monkeys. Monkey L1 was an immature male with a small accessory on the right side (Fig. 4). The accessory nipple and the left normal one were painted daily with an alcoholic solution of estrone, 0.05 mg. per c.c., for 44 days. The right normal nipple was used as a control and was painted daily

with plain alcohol. The results of treatment are shown in Fig. 5 and 6. There was a distinct increase in size and color of the supernumerary nipple, but the growth was somewhat less than that attained by the left normal nipple. This suggests that the supernumerary nipple, although responsive to estrogenic hormone, is either not as sensitive or lacks the same capacity for growth as the normal nipple.

Monkey no. 708 was a mature female with a large accessory nipple on the right side, of approximately the same size as the normal nipple. This



FIG. 3. MONKEY NO. 313. WHOLE MOUNT OF SUPERNUMERARY MAMMARY GLAND, CONSISTING OF ONLY TWO SHORT DUCTS; SHOWING RELATION TO LOWER BORDER OF LEFT NORMAL MAMMARY GLAND

Alum cochineal; $\times 3$.

animal was similarly treated with local application of estrogenic hormone to the accessory nipple, but there was no demonstrable increase in size. This may possibly be explained on the basis of the nipple's having attained its maximal growth before treatment was begun. When the mammae were dissected a well-developed gland, with extensive arborization of the ducts and many end-buds, was found underlying the supernumerary nipple. This was the largest supernumerary gland in the entire series, and it extended to the lower border of the ipsilateral normal gland. It is possible that the accessory gland may have attained this size independently of the treatment. It has recently

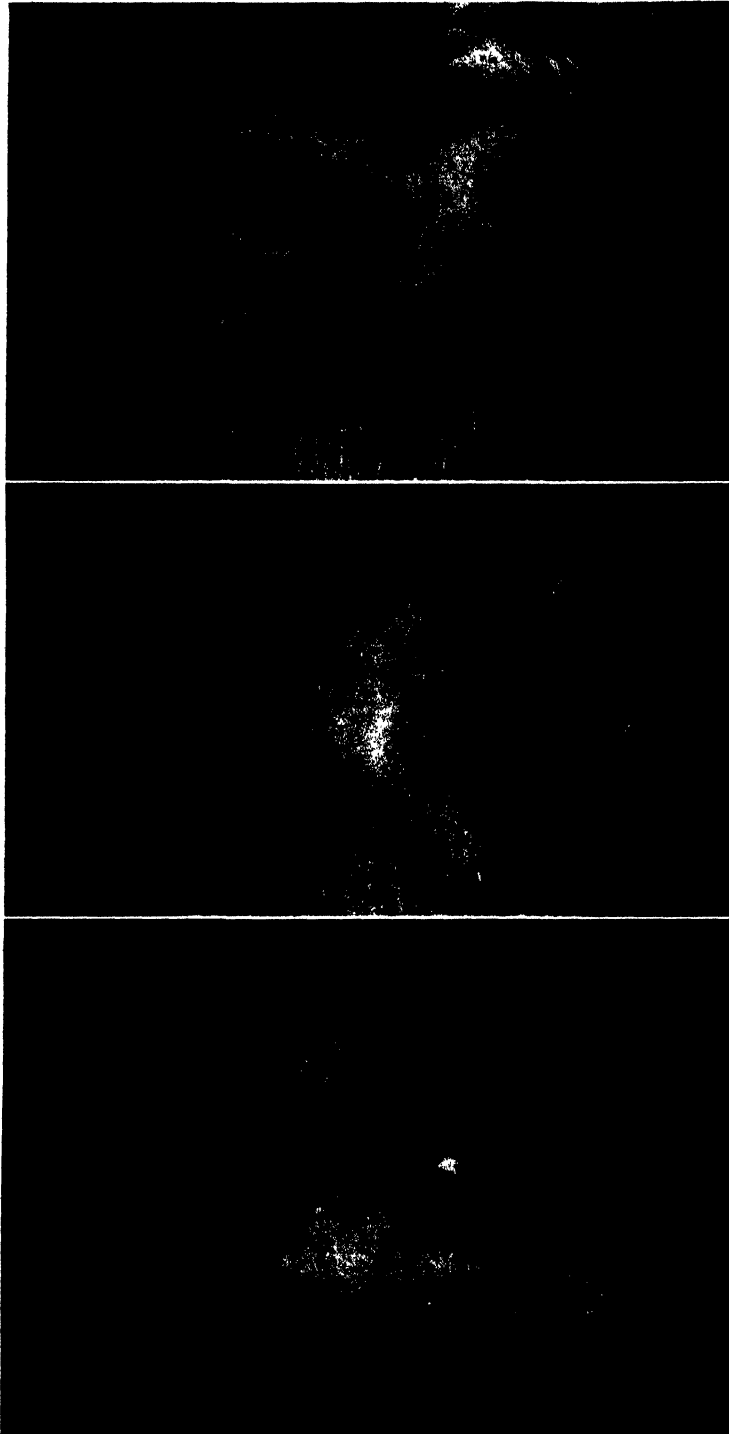


FIG. 4-6. MONKEY L1, IMMATURE MALE. EFFECTS OF DAILY APPLICATION OF ALCOHOLIC SOLUTION OF ESTRONE 0.05 mgm. per c.c., to left nipple and to right supernumerary, for forty-four days. The right normal nipple was treated with plain alcohol.

Fig. 4 (top). Before treatment. Figs. 5 (center) and 6 (bottom). After treatment.

been found, however, (Speert, 1940) that localized parenchymal growth of the monkey mammary gland may be affected by the application of estrogenic hormone to the nipple area, and it is likely that this treatment was responsible for the extensive glandular development observed.

SUMMARY

The occurrence and significance of supernumerary mammae in the human have been discussed, with special regard for the various views which have been held concerning their etiology, and for the statistical data which have been amassed relating to their incidence and location. The hereditary aspects of polymastia and polythelia are reviewed, and the theories associating these anomalies with fecundity and multiple births, tuberculosis, left-handedness, and congenital abnormalities are discussed. Some clinical aspects of this condition are also briefly mentioned.

The reported instances of accessory nipples in sub-human primates are reviewed. Only two cases have been observed previously in the rhesus monkey, and thirteen more are reported for this species. The incidence of supernumerary nipples in the rhesus monkey was found to be approximately 1.4 per cent, a figure in agreement with most recent estimates of the incidence of this condition in the human. Eleven of the thirteen animals in the present series had unilateral supernumerary nipples; in two the supernumeraries were bilateral. Supernumerary nipples were observed with about the same frequency on the two sides of the body. In only five instances was accessory glandular tissue associated with the accessory nipples.

Supernumerary nipples were found capable of responding, by growth and increased color intensity, to the local application of estrogenic hormone.

LIST OF LITERATURE

- AHLFELD, F. 1880. Die Missbildungen des Menschen. *Leipzig*, s. 110.
- BARDELEBEN, K. 1891. Die Häufigkeit überzähliger Brustwarzen (Hyperthelie), besonders beim Manne *Verhandl. d. anat. Gesellschaft., Jena*, Bd. 5, S. 242-250.
- . 1893. Massenuntersuchungen über Hyperthelie beim Manne. *Verhandl. d. anat. Gesellschaft., Jena*, Bd. 7, S. 171-185.
- BEDDARD, F. E. 1901. *Proc. Zool. Soc. Lond.*, vol. 1, pp. 87-88.
- BELL, A. G. 1923. Saving the six-nippled breed. *J. Hered.*, vol. 14, pp. 99-111.
- BIRKENFELD, W. 1932. Beitrag zur Zwillingspathologie der Mamma. *Arch. f. klin. Chir.*, 1932. Bd. 168, S. 568-576.
- BOENHEIM, F. 1919. Über das Vorkommen überzähliger Mamillen und Kombination derselben mit anderen Degenerations-Zeichen. *Anat. Hefte*, Bd. 57, Abt. 1, S. 583-609.
- BONNET, R. 1892. Die Mammorgane im Lichte der Ontogenie und Phylogenie. *Anat. Hefte*, Bd. 2, Abt. 2, S. 604-658.
- BRESSLAU, E. 1909. Der Mammarapparat. *Anat. Hefte*, Bd. 19, Abt. 1, S. 275-349.
- BRUCE, J. M. 1879. On supernumerary nipples and mammae; with an account of sixty-five instances observed. *J. Anat. and Physiol.*, vol. 13, pp. 425-448.
- CASTLE, W. E. 1924. The genetics of multi-nippled sheep. *J. Hered.*, vol. 15, pp. 75-85.
- CHAMPNEYS, F. H. 1886. On the development of mammary functions by the skin of lying-in women. *Med.-Chir. Tr., Lond.*, vol. 69, pp. 419-442.
- DE CHOLNOKY, T. 1939. Supernumerary breast. *Arch. Surg.*, vol. 39, pp. 926-941.
- COOLIDGE, H. J., JR. 1933. Symmetrical supernumerary mammae in a chimpanzee. *J. Mam-mology*, vol. 14, pp. 66-67.
- DARWIN, C. 1868. The variations of animals and plants under domestication. *London*, vol. 2, p. 57.
- . 1871. The Descent of Man. *New York*, Pt. 1, p. 120.
- DEAVER, J. B., and MCFARLAND, J. 1917. The Breast: Its Anomalies, Its Diseases, and Their Treatment. *Philadelphia*, pp. 51-101.
- ELDER, J. H. 1936. Report of a case of inherited polymastia in chimpanzee. *Anat. Rec.*, vol. 65, pp. 83-88.
- FLECHSIG, R. 1840. Ueber Polymastie oder die Vielbrüstigkeit bei Menschen. *Neue Ztschr. f. Geburtskunde*, Bd. 9, S. 12-74.
- GEOFFROY SAINT-HILAIRE, M. I. 1832. Histoire générale et partic. des anomalies de l'organisation chez l'homme et les animaux. *Paris*, T. 1, p. 710.
- GRAHAM-CAMPBELL, R. 1936. Polythelia. *Brit. M. J.*, Pt. 1, p. 471.
- HANDYSIDE, P. D. 1873. Notice of quadruple mammae,—the lower two rudimentary,—in two adult brothers. *J. Anat. and Physiol.*, vol. 7, pp. 56-59.
- HANSEMANN, D. 1889. Ueber Polymastie. *Ver-handl. d. Berl. Gesellsch. f. Anthropol.*, S. 434-443.
- HARTMAN, C. G. 1927. A case of supernumerary

- nipple in *Macacus rhesus*, with remarks upon the biology of polymastia and polythelia. *J. Mammology*, vol. 8, pp. 96-106.
- HATHAWAY, J. H. 1909. Occurrence of supernumerary nipples in the male, based on an examination of college students. *Anat. Rec.*, vol. 3, pp. 265-267.
- HIRSCHLAND, L. 1898. Beiträge zur ersten Entwicklung der Mammarorgane beim Menschen. *Anat. Hefte*, Bd. 11, Abt. 1, S. 221-243.
- HIRST, B. C. 1912. A Text-Book of Obstetrics. Seventh ed. *Philadelphia*, p. 706.
- HOEFFNER, L. 1899. Über Vorkommen und mikroskopisches Verhalten überzähliger Brustwarzen beim Menschen, besonders beim Manne. Inaug.-Diss., *Jena*.
- HUG, J. 1908. Sitz und Vorkommen überzähliger Brustdrüsen und Brustwarzen beim Weibe. Inaug.-Diss., *Strassburg*.
- IWAI, T. 1906. In Editorial, "Polymastie et tuberculose." *Presse méd.*, T. 14, p. 650.
- . 1907a. A statistical study on the polymastia of the Japanese. *Lancet*, Pt. 2, pp. 753-759.
- . 1907b. Relation of polymastia to multiparous birth. *Lancet*, Pt. 2, pp. 818-820.
- . 1907c. Relation of polymastia to tuberculosis. *Lancet*, Pt. 2, pp. 958-960.
- KAJAVA, Y., SCHRODERUS, M., WALLENUS, M., and WICHMANN, S. E. 1921. Das Vorkommen überzähliger Milchdrüsen bei der Bevölkerung in Finland. *Acta Soc. med. fenn. duodecim.*, Bd. 2, S. 1-163.
- KAYSER, F. 1908. Achselhöhlenbrüste bei Wöchnerinnen. *Arch. f. Gynäk.*, Bd. 85, S. 459-482.
- KLINKERFUSS, G. H. 1924. Four generations of polymastia. *J. A. M. A.*, vol. 82, pp. 1247-1248.
- LAMAR, J. K. AND SPEERT, H. Unpublished.
- LANDAUER, W. 1939. Supernumerary nipples, congenital hemihypertrophy and congenital hemiatrophy. *Human Biol.*, vol. 11, pp. 447-472.
- LEICHTENSTERN. 1878. Über das Vorkommen und die Bedeutung supernumerärer (accessorischer) Brüste und Brustwarzen. *Virchows Arch. f. path. Anat.*, Bd. 73, S. 222-256.
- MARIE, M. P. 1893. Mamelon surnuméraire transmis héréditairement dans une famille; coïncidence avec plusieurs grosses gémellaires; reversion atavique à—ou création d'un—type polymastie et polygène (?). *Bull. et mém. Soc. méd. d. hop. de Par.*, T. 10, pp. 457-459.
- MCGILLICUDDY, T. J. 1891. The mammae and their anomalies. *Med. Rec.*, vol. 40, pp. 446-449.
- MECKEL VON HEMSBAACH, H. 1852. Pathologische Anatomie der Brustdrüse. *Illust. med. Ztg.*, Bd. 1, S. 141-155.
- NEUGEBAUER, F. L. 1886. Ein bisher einzig dastehende Beobachtung von Polymastie mit 10 Brustwarzen. *Centralbl. f. Gynäk.*, Bd. 10, S. 729-736.
- OWEN, R. 1886. Anatomy of Vertebrates. *London*, vol. 3, p. 780.
- PÉTRIGNANI, R. 1939. Polymastie et gémellité. *Bull. Soc. gynec. et d'obst.*, T. 28, pp. 306-307.
- RITZMAN, E. G. 1933. The multinipple trait in sheep and its inheritance. *New Hamp. Exp. Sta. Tech. Bull.* 53.
- SATO, K. Quoted by Iwai, T. 1907a. *Lancet*, Pt. 2, pp. 753-759.
- SCHICKELE, G. 1899. Beiträge zur Morphologie und Entwicklung der normalen und überzähligen Milchdrüsen. *Ztschr. f. Morphol. u. Anthropol.*, Bd. 1, S. 507-546.
- SCHMIDT, H. 1897. Ueber normale Hyperthelie menschlicher Embryonen und über die erste Anlage der menschlichen Milchdrüsen überhaupt. *Morphol. Arb.*, Bd. 7, S. 157-199.
- SCHMITT, H. 1898. Ueber die Entwicklung der Milchdrüse und die Hyperthelie menschlicher Embryonen. *Morphol. Arb.*, Bd. 8, S. 236-303.
- SCHULTZE, O. 1892. Ueber die erste Anlage des Milchdrüsenapparates. *Anat. Anz.*, Bd. 7, S. 265-270.
- SEITZ, L. 1909. Ueber die sogenannte Achselhöhlenmilchdrüse und deren Genese; Schwangerschafts-metamorphose der Schweißdrüsen. *Arch. f. Gynäk.*, Bd. 88, S. 94-131.
- SPEERT, H. 1940. Mode of action of estrogens on the mammary gland. *Science*, vol. 92, pp. 461-462.
- STANNUS, H. S. 1914. Congenital anomalies in a native African race. *Biometrika*, vol. 10, pp. 1-24.
- STIER, E. 1912. Ueber Hemiatrophie und Hemihypertrophie nebst einigen Bemerkungen über ihre laterale Lokalisation. *Deutsche Ztschr. f. Nervenhe.*, Bd. 44, S. 21-64.
- SUTTON, J. B. 1889. Supernumerary mammae and nipples in man, monkeys, cows, etc. *Am. J. M. Sc.*, vol. 97, pp. 247-257.
- TIFFANY, L. M. 1901. In Ref. Handb. Med. Sc., vol. 2, pp. 471-472.
- WALTER, H. E. 1902. On transitory epithelial structures associated with the mammary apparatus in man. *Anat. Anz.*, Bd. 22, S. 97-111.
- WEITZ, W. 1925. Studien an einseitigen Zwillingen. *Ztschr. f. klin. Med.*, Bd. 101, S. 115-154.
- WIEDERSHEIM, R. 1908. Der Bau des Menschen als Zeugnis für seine Vergangenheit. *Tübingen*, S. 23-37.
- WILLIAMS, W. R. 1894. Diseases of the Breast. *New York*, pp. 43-81.
- WOODMAN, W. B. 1868. Three cases of a third nipple in the human subject—one case hereditary. *Tr. Obst. Soc. Lond.*, vol. 9, pp. 50-51.
- ZUCKERMAN, S. 1935. Supernumerary nipples in monkeys. *J. Mammology*, vol. 16, pp. 229-230.



NEW BIOLOGICAL BOOKS

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BIOGRAPHY OF A STATESMAN

Being a review of *William Henry Welch and the Heroic Age of Medicine* by Simon Flexner and James Thomas Flexner. New York (The Viking Press), 1941. 9½ x 6½; x + 539. \$3.75.

By *William Travis Howard, Baltimore, Maryland.*

This work, authoritative, well-arranged, and written *con amore*, is easy reading. The text is not marred by footnotes, references to the sources being given conveniently in an appendix.

Fortunate in life, Welch is also fortunate in his biographers who, fortified by a wealth of material and a long and intimate association, portray over a period of eighty-four years the progressive development of a great personality under a rapidly changing environment in science, medicine, hygiene, and social conditions. With absorbing interest they trace the evolution of the man, intellectually, spiritually, and socially, and step by step they indicate the paths which led up to the commanding rôle he played in the changes for the better, especially in medicine and hygiene, from the crude conditions of 1870 to those we now enjoy.

Of those now living who had the privilege of associating with Welch, many will find here details of his life with which they were unacquainted; others will be disappointed that some of his characteristics which they particularly valued are not more fully stressed; and still others will doubtless think that undue space is given the minutiae concerning the development of medicine and medical teaching during Welch's life time and the numerous scientific and philanthropic organizations which he served and to such a great extent guided. However, this is a matter of judgment in method and selection with which this reviewer finds himself in sympathy.

Born in 1850, in Norfolk, Connecticut, in the beautiful Litchfield Valley, Welch sprang on the paternal side from sturdy stock abundantly identified with

medicine. Besides his father, two great uncles and four uncles were physicians. Welch's father, a successful physician well in advance of his time, served his community in the State Legislature and in the United States House of Representatives and was interested as well in banking and manufacture. His mother, of Huguenot extraction on her father's side, was a woman of talent and distinct literary gifts. Delicate in health, she died early, leaving a daughter of two and a half years and William Henry, aged six months.

Cared for by his grandmother, a deeply religious woman, until his fourteenth year, Welch was sent to boarding school and thence to Yale where he made his mark, graduating in 1870, second in his class.

It is a far cry from the rural Connecticut boy, indoctrinated in the then current Jonathan Edwards brand of religion, who in his college days was the author of the "Decay of Faith," to the natural scientist of maturer years, the exemplar of critical analysis of closely observed facts, tested and expanded by controlled experiment where possible and the whole submitted to the strict forms of logic, who in his old age kept Rabelais's works on his bedside table.

Disappointed on graduation in obtaining a tutorship in Greek, his favorite study, and after teaching school for two years, with great reluctance young Welch became apprenticed to his father in medical practice. In 1872 he returned to Yale for a course in laboratory chemistry, and the following fall he entered on medical studies at the College of Physicians and Surgeons in New York where he won distinction. Here he was particularly interested in normal and pathological anatomy and neurology. Even before graduating in 1875 and prior to the formal opening of the Johns Hopkins University, young Welch visited Baltimore to seek an appointment in pathology. Throughout his several years of study in chemistry anatomy, physiology, pathological anatomy, and gen-

eral pathology in Strassbourg, Leipzig, and Breslau under some of Germany's leading masters in these subjects and later during his early struggles in teaching pathology in New York, Welch ever had this goal in mind. During these student years, he found time to indulge his taste for music, painting, and architecture, and thus laid the foundation for the deep interest in general culture which later opened the door for associations and friendships of the most diverse types. With his fine and well-disciplined mind and his broad training, Welch was *facile princeps* among the younger men interested in the scientific side of medicine in America when, having attained the coveted professorship of pathology in the new University, he opened his laboratory in Baltimore and set to work to introduce to his native land the methods of teaching and investigation of the German universities.

With but little hesitation, he put behind him the lure of money-mart medical practice and social distinction in New York to undertake the inauguration of pathology as a scientific discipline in an infant university in a provincial town.

Welch was a man of general rather than special talent, who could have made his mark in any one of several fields. With a consuming curiosity for knowledge, he spread his talents over a variety of interests: science, literature, pictorial and plastic art, music, and architecture. A master of the techniques of anatomy, physiology, pathological anatomy, general pathology, bacteriology, and animal parasitology, he invented no new methods opening up avenues of discovery in any of his chosen interests.

His happiest years were probably those between 1884 and 1894 when, free from administrative duties and outside demands and surrounded by an enthusiastic band of talented associates and pupils, he was prosecuting and stimulating productive research. The senior author's description and evaluation of Welch's scientific contributions and teaching methods constitute a valuable section of the book.

The organization of the Medical School was the opening wedge between Welch and his beloved laboratory, and by the turn of the century, he had become a national figure, and his abilities and energies were swept, perhaps against his will, into a rapidly growing multitude of outside activities: medical and scientific societies, foundations for scientific investigation, and philanthropic institutions—local, national, and international. These activities involved much travel and the delivery of innumerable addresses, many of which were written overnight on trains.

Significant of Welch's dominating influence upon the Johns Hopkins Hospital in the early days is the fact that although the clinical departments were presided over by such talented and individualistic men as Halsted, Osler, and Kelly, the tone of the institution was set by the pathological laboratory. Indeed, perhaps the most striking feature of the research upon

which the reputation of the Hospital was so largely based was its close coordination of the clinic with the laboratory. Halsted who worked out his aseptic technique in the laboratory and his assistant, Cushing, were experimental pathologists of note. Osler was a trained pathological anatomist, and his early residents, Lafleur and Thayer, had tables in the Pathological. From Kelly's Clinic, Whitridge Williams, Robb, Griskey, and Cullen made important contributions in the bacteriology and pathology of the female generative organs. With every phase of the work of both clinic and laboratory, Welch was in intimate touch.

Nor when the medical school opened with brilliant and productive heads of the laboratories of anatomy, physiology, and pharmacology, did the pathological laboratory under Welch suffer by comparison.

After most men retire, Welch established two new schools in the Johns Hopkins University—the School of Hygiene and Public Health and the Institute of the History of Medicine. Here he showed the same judgment and breadth of view which marked the organization of the medical school. Asking nothing for himself, he never strained his great influence to further his own University above other interests. Although meticulously careful of even the minutest details in his investigations and his editorial functions, in the administration of his laboratory and of the various schools he organized in the University and in his numerous outside activities the details were left to others.

Very popular with women and holding them in high regard, he remained celibate. Welcomed in many homes, he never had one of his own, preferring to live in "rooms" (bedroom, bath, and study), always near his clubs where he took his meals and did his frequent entertaining.

A gap in the narrative, which, to a certain degree, the present reviewer can fill, concerns Welch's associates, medical and social, during his early years in Baltimore. His association with President Gilman, while cordial, was never intimate. Indeed, Gilman had no intimates, and his position in Baltimore was one of aloofness. Having picked his men and given them opportunities, he left them free. Among the faculty of the natural sciences, with Remsen, the chemist, Rowland, the fox-hunting physicist, and Brooks, the talented but retiring zoologist, Welch's relations were friendly but not close. His cousin, Huntington Williams, who urged him to accept the Hopkins offer, died only too soon. Considering Welch's early love of Greek, it seems strange that Gildersleeve and he were not close associates. Newell Martin, head of the Department of Biology, whose laboratory gave space to Welch during his first year in Baltimore, was perhaps his only intimate on the faculty. Yet, Welch's secondary motive in accepting the Hopkins Chair was for comradeship with men of this type. However, all his colleagues with the ex-

ception of Gildersleeve were absorbed in their own pursuits with their reputations to make, and all except Martin were married. Furthermore, Welch at once fell under two influences which affected his after life in Baltimore. In the first place, he was elected to membership in the then exclusive Maryland Club the members of which represented the Maryland aristocracy in birth, breeding, and accomplishment, with a sprinkling of men of similar qualities from without the State, chiefly from Virginia and South Carolina. He was probably proposed by Doctor Alan P. Smith, grandson of the founder of the Yale Medical School, a surgeon of distinction, and the only physician appointed by Johns Hopkins on the original Board of Trustees of the Hopkins Hospital. Welch's "rooms" were near the Club and within a stone's throw of the homes of many of the leading medical men. At the Club, he associated not only with influential physicians but with several of the trustees of the University and Hospital, including Judge Dobbin, President of the Board. Here he met Major Richard Venable, eminent lawyer, cultivated Virginia gentleman, unreconstructed rebel, and boisterous wit, who with Halsted became the men dearest to his heart.

Almost immediately Welch was adopted by the medical profession of Maryland; at the first vacancy he was elected to the Medical Reunion, a supper club composed of the leading physicians, and within five years he was chosen president of the Medical and Chirurgical Faculty of Maryland, an honor reserved for the most distinguished among the membership.

From the very start of his Baltimore life, Welch was received socially and professionally with open arms and thus early was his universality recognized. Of jealousy there was none, and his popularity in ever spreading circles never waned.

Halsted, his friend of the New York days, joined him in 1886, took rooms next door, and belonged to the same circle at the Maryland Club.

In the early days of the Hopkins Hospital, the medical profession was justly antagonistic. But the authors are quite excusably in error in attributing this to the fact that three outsiders were chosen for the principal clinical posts. All the active heads of the various departments and their assistants in the dispensary, were Baltimoreans. Some like Theobald, McKenzie, Booker, James Brown, and Morison, were leaders in their specialties with national reputations. In obstetrics, gynecology, and surgery, the leading local men were too old even if asked to have undertaken the burden. In medicine, there was only one man, I. E. Atkinson, who might have reasonably aspired to a principal chair. Halsted, in surgery, was hardly an outsider. He had been working in Welch's laboratory for three years, and having no office could not be looked upon as a competitor. The antagonism had its source in two circumstances: What was considered President Gilman's over fulsome praise of Oiler and Kelly, and,

much more important, the dispensary was soon flooded with patients able and accustomed to pay their physicians. These grievancies were soon assuaged by the appointment of a number of the leaders in the profession as consultants to the Hospital and by better control of the dispensary clientele.

As had been the case with Welch's laboratory, the dispensary services and clinics of Halsted, Oiler, and Kelly soon became the Mecca of the younger men of the profession.

Welch's career is unique in American medicine. Distinguished for his scientific contributions, his influence as a teacher and organizer of three different departments in the University, he was in the correct sense of the term a great statesman. This country has produced two other men who similarly and justly attained universal respect and beneficent influence in homage to their minds, characters, and attainments, and their unselfish devotion to the public interest in their respective fields of activity. In following Welch's career, one is tempted to think of him as a happy combination of these two philosophers—Franklin and Jefferson. Welch was of much the same body build as Franklin and was endowed with the same vigor and capacity for hard work. He possessed the same insatiable and universal mental curiosity, the love of learning, the bonhomie, the poise, the patience, and the wisdom so characteristic of Franklin. Like the latter, he attained world-wide reputation in natural science, and like him, too, even up to the end of life, he was constantly called on to advise and to guide new movements. Like Franklin, also, Welch combined geniality and hospitality with personal dignity and was above self-seeking and jealousy. The honors that came to both were unsought and were borne with becoming modesty. Like Jefferson, Welch loved all that is elegant in life and beautiful in nature and art. They shared the same aspirations for the improvement of mankind and exercised the same caution against proceeding faster in reform than conditions seemed to warrant. In Jefferson's milieu, Welch might well have written the bill of religious freedom, have planned a system of education based on the free grammar school, the county academy at which exceptionally brilliant boys would be supported at public expense, all topped by a state university, presided over by scholars, in which the students attended the "schools" of their choice in any order they chose. Similarly, Welch might well have obtained vaccine virus from Waterhouse and in the Montecello neighborhood, without medical assistance, have made observations on the evolution of the lesions of vaccinia which for preciseness are unsurpassed. As Jefferson was the political "Sage of Montecello," so Welch became the "Medical Sage of St. Paul Street," to whom came persons from near and far seeking advice in education, medicine, hygiene, and philanthropy.

By those now living, who knew and loved Welch, this account of his life will be received with gratitude. Those who knew of him only as a great man will learn wherein his greatness lay. Biologists will greet a great biologist. All readers will recognize not only an energetic, forceful character, but a wise, generous, and lovable man who more than deserved the unique national and international tributes paid him on his

eightieth birthday, and will understand why Venable on his deathbed said, "I want to express my admiration for Doctor Welch," and why Halsted said on a great occasion given in his own honor, "All that I have accomplished in my scientific investigations I owe to the example and guidance of Doctor Welch," and why Councilman once said, "I would lay down my life for Welch."

BRIEF NOTICES

EVOLUTION

A MIOCENE FLORA FROM SHANTUNG PROVINCE, CHINA. Part I. *Introduction and Systematic Considerations. Part II. Physical Conditions and Correlation.* Carnegie Institution of Washington Publication No. 507. *Contributions to Paleontology.*

By Hsen Hsu Hu and Ralph W. Chaney. Carnegie Institution of Washington, D. C. \$3.75 (cloth); \$3.25 (paper). 11½ x 8½; vi + 147 + 57 plates; 1940.

Previous to 1938 there had been no known record of the occurrence of rock of Miocene age in China proper. The discovery of deposits near Shanwang in Shantung Province have yielded large collections of fossil plants, insects, fish, frogs, turtles, and mammals. A study of the shales and the physical conditions of the region, past and present, has produced results of great significance, not only in the Tertiary history of Asia but in the history of the development of vegetation throughout the northern hemisphere. The presence of aquatic plants and numerous fish shows that the shales were largely deposited in lakes. All evidence seems to point to the Shanwang formation as being late Miocene. "It appears to have accumulated during the time units referred to the Saratian in Europe, and Mascall to San Pablo in North America."

The flora as now known is made up exclusively of angiosperms. Environmental factors seem to account for the absence of coniferous genera which are regularly present in the Tertiary floras of China, Japan, and Siberia. Omitting the herbs, which form a small portion of the flora, the ratio of trees to shrubs is 45 to 55. This relationship is "extremely high for a flora containing so many temperate genera, and corresponds to that of the tropical forest near Manila. The relatively large proportion of vines is a characteristic of warm, moist habitats."

The 50 plates accompanying the systematic part of this study give a fine pictorial record of the flora from the deposits. The seven plates in the second part show topography and modern vegetation in the immediate vicinity of the fossil locality and elsewhere in North China and Japan. Both parts are well documented.

SPECIATION IN THE AVIAN GENUS JUNCO. *University of California Publications in Zoology, Volume 44, Number 3.*

By Alden H. Miller. University of California Press, Berkeley and Los Angeles. \$3.00. 10½ x 6½; 262; 1941 (paper).

In this exhaustive review of the genus *Junco*, the writer has not formulated his conclusions on museum specimens alone, as is usually the case in most works of this nature, but has supplemented his data with actual field observations. The yellow-eyed juncos consist of the *alticola* and *phaenotus* groups (*artenkreise*), and the dark-eyed birds fall into the *oreganus* and *hyemalis* groups with the *caniceps* (*rassenkreise*) intermediate between the former two. In all groups there is a good correlation between wing and tail length; no other correlations of large magnitude run through all forms of juncos with constancy. No environmental correlation of color (Gloger's Law), of size (Bergmann's Law), or of size of extremities (Allen's Law) could be found.

As to the phylogeny of the genus, it appears that it arose in North and Middle America and now shows no resemblance to the Emberizinae of Europe and South America. *Vulcani* is considered a primitive stage followed by the yellow-eyed juncos. *Caniceps*-like and *hyemalis*-like forms may have arisen at the same time in the interior and in the East.

Each taxonomic form is carefully described, the range outlined, intraracial and interracial variations, and relationships discussed. The first appendix is a comprehensive review of the nomenclature, and the second lists the breeding localities of typical populations. Altogether this forms a notable contribution for a better understanding of a difficult group of birds.



PREHISTORIC COMMUNITIES OF THE BRITISH ISLES.

By V. Gordon Childe. W. and R. Chambers, London and Edinburgh. 20s. net. 9 x 6½; xiv + 274 + 16 plates. 1940.

Although paleolithic sub-men have occupied the British Isles for approximately half a million years, it was only about fifty thousand years ago that men who can be definitely identified as *Homo sapiens* ap-

peared. The cultural remains of these earlier inhabitants is not adequate for the recognition of the graded stages of development such as occur in France. The earliest culture that can be correlated with a corresponding one from the continent is the Aurignacean, but this was not developed spontaneously but was introduced from the mainland.

All subsequent cultures are amply represented in Britain by such structures as barrows, cairns, brochs, etc., which are more numerous than commonly supposed. Excavation of these has yielded a great quantity of stone and clay shards, knives and spear points, urns and beakers, and from later times bobbins, bits, dice, and coins.

In the present work all of these artifacts are discussed in detail, as well as those of the pre-Aurignacean cultures. Numerous text figures and diagrammatic maps elucidate the text, and a series of excellent plates from photographs by the author add to the value of the book. Even the pre-Romanic languages come in for a share of the discussion. Of these there appear to have been seven, six of which have Keltic affinities while the relationships of the seventh, which is probably the oldest, are unknown.

The book is complete and scholarly, with extensive index and bibliography.



MAMMALS OF THE LAVA FIELDS AND ADJOINING AREAS IN VALENCIA COUNTY, NEW MEXICO. *Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 51.*

By Emmet T. Hooper. University of Michigan Press, Ann Arbor. 50 cents. 10 x 6½; 47 + 3 plates; 1941 (paper).

A report of a study of the mammal fauna of a section of west-central New Mexico on and around extensive fields of blackish lava to determine the forces directing the evolution of dark races of mammals on the lava flows. In the Tularosa Basin, where the lava beds are much more isolated than those in Valencia County, the blackish pelage coloration has become more completely fixed. The study, based on records of 60 kinds of mammals (species and subspecies) indicates "(1) that the darker coloration has a higher survival value on the black lava; and (2) that the present center of dispersal of the darker animals is the black lava and not the lighter substrata near the black lava."



DEVELOPMENT OF OCCLUSION. *University of Pennsylvania Bicentennial Conference, M-12.*

By William K. Gregory, B. Holly Broadbent, and Milo Hellman. University of Pennsylvania Press, Philadelphia. \$1.50. 9 x 6; 72; 1941 (paper).

GENETICS

GENETICS AND THE ORIGIN OF SPECIES. Second Edition, Revised.

By Theodosius Dobzhansky. Columbia University Press, New York. \$4.25. 9 x 6; xviii + 446; 1941.

The first edition of this outstanding book has already been reviewed in this journal (Vol. 13, p. 211). The second edition does not need a detailed review, for the author's point of view and his arrangement of the material has remained essentially the same. Nevertheless a considerable number of additions and some changes have been made, and these deserve notice.

While most of the minor changes are the result of the author's desire to make the text more explicit, the most important changes are additions of new material. This is exemplified by the increase in the number of references from about 600 to nearly 1,000 and of the number of pages from 364 to 446. The inclusion of so much new material is the result on the one hand of the recent growth of research on evolutionary problems and on the other of the expansion of the author's interests. The inclusion in the revised edition of work on the transformations of pneumococci is a good example of this. Some changes in the arrangement of the material have been made of which the most noticeable is a shift of the material on the theoretical significance of population dynamics from the chapter on selection to a new chapter entitled "Patterns of Evolution."

Among the recent works on evolution discussed and criticized by Dobzhansky, Goldschmidt's *The Material Basis of Evolution* takes a prominent place. This is not surprising since the two authors differ even in some of their basic assumptions.

A revision at the present time of Dobzhansky's excellent book would have been welcomed in any case by biologists interested in evolution. Perhaps some of them will find it particularly valuable because it follows so closely the expression of very different views by Goldschmidt.



GENERAL BIOLOGY

BIOLOGY AND HUMAN AFFAIRS.

By John W. Rüschie. World Book Company, Yonkers-on-Hudson. New York. \$2.32. 8½ x 5½; xiv + 1026; 1941.

The encyclopedic proportions of this high school textbook (1026 pages) may at first glance frighten away some of those for whom it is intended. However, although much more material has been included than an average class can hope to cover in one year, the 22 units are, in the main, independent of each other so that they can be taken up in practically any order, or some can be omitted. The point of view is practical

throughout, the wide application of biological ideas to human living being constantly emphasized.

The teaching method combines the type, group, and principles methods. The number of scientific terms has been kept at a minimum. The author is to be especially commended for the excellent and profuse illustrations which are a distinct feature of the book. Each unit is concluded with a comprehension test, a list of suggested activities and applications, and selected references for reading. The appendix contains a classification of animal and plant kingdoms, a table of the divisions of geological time, a complete glossary, and an index.



EXPLORATIONS AND FIELD-WORK OF THE SMITHSONIAN INSTITUTION IN 1940. *Smithsonian Institution Publication 3631.*

Smithsonian Institution, Washington, D. C. Free. 9½ x 6; 100; 1941 (paper).

Each year expeditions go out from the Smithsonian Institution to collect specimens, record data, etc. in the various fields of science. A preliminary announcement of the year's work is issued in pamphlet form. The present report shows that, as usual, much work was done in the biological sciences in 1940. Early man was traced in Virginia and Folsom man in the West, while various Indian groups in North America were studied. Live animals were collected in Liberia while extinct animals were trailed in the central Utah and the Bridges Basin of Wyoming. Grasses were studied in Venezuela, butterflies in Virginia, birds and mammals collected in South Carolina, and reptiles and amphibians in Mexico. Habitat group material was collected in the Canadian Rockies, dredge hauls made in the Gulf of California and the King crab (what we know in canned form as Japanese crab meat) studied in Alaskan waters. The many photographs form an interesting part of this brief report.



AN INTRODUCTION TO BIOLOGY.

By J. C. Cross. *The C. V. Mosby Company, St. Louis.* \$1.90. 7½ x 5½; xviii + 507; 1941.

This book has been written for the special purpose of presenting southern plants and animals to students and teachers of high schools in that part of the country. Since southern fauna are rich enough to supply good examples for nearly all practical purposes, either for laboratory or for recitation, the author selected those representative forms of the biological resources of the South that would be of most value in a high school course. The textual material is divided into eight parts or units. In general, the book follows the plan of proceeding from the simpler plants and animals to

the more complex. The divisions of the material are as follows: Introduction; The simplest animals; Plants without seeds; The seed-bearing plants; Animals with jointed feet; Animals with backbones; Structure and function in plants; and Structure and function in animals. There is no bibliography but an excellent glossary and index are available.



OCEANOGRAPHY OF THE NORTH PACIFIC OCEAN, BERING SEA AND BERING STRAIT: *A Contribution toward a Bibliography.*

By Mary C. Grier. *University of Washington, Seattle.* \$2.50. 19 x 7; xxii + 290; 1941 (paper).

More than 2,930 items are listed in this bibliography. Important books, magazine articles and documents bearing upon the oceanography of the area defined and the inshore waters, with the exception of the coast of California, are given. The bibliography is divided into the following sections: General references, Physical oceanography, General biology, Plankton, Invertebrata, Pisces, Aves, Mammalia, and Flora. There are indexes to author and personal names and to subjects and titles. The volume is well printed. The generous spacing of the items not only makes for easy reading but gives opportunity to the student to jot down additional notes.



PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE, ARTS AND LETTERS. *Volume XXVI (1940). Part I: Botany and Forestry. Part II: Zoology. Part III: Geography and Geology.*

Edited by Eugene S. McCartney and Mischa Titiev. *The University of Michigan Press, Ann Arbor; Oxford University Press, London.* Part I, \$1.75; Part II, \$1.75; Part III, \$1.50. 9½ x 6; Part I, vii + 158 + 3 plates; Part II, viii + 180 + 1 plate; Part III, vii + 104 + 1 plate; 1941 (paper).

Volume 26 of this series is available in four parts; the first dealing with botany and forestry, the second with zoology, and the third with geography and geology. The fourth part is concerned with topics in other than biological fields. The contributions are too numerous to mention even by subject matter. They pertain mostly to the biology of Michigan.



CINE-BIOLOGY.

By J. V. Durdan, Mary Field and F. Percy Smith. *Penguin Books, Harmondsworth, Middlesex, England; Penguin Books, Inc., New York.* 25 cents. 7 x 4½; 128; 1941 (paper).

"...an attempt to blend together into one narrative three sharply contrasting points of view; these are the

critical accuracy of the scientist, the exuberant enthusiasm of the naturalist, and the anthropomorphic ideas of the layman who strives to translate the doings of an insect in terms of human endeavour." For this purpose the common invertebrates have been chosen.

The illustrations are from photographs (hence Ciné-biology?). The result is pleasing and readable and should be enjoyed by the layman for whom it is intended.



COLLECTED REPRINTS: 1940. Woods Hole Oceanographic Institution: Containing also the Annual Report of the Director of 1939.

By Various Authors. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts. \$3.00. 9½ x 7; 1941 (paper).

This volume contains those contributions from the Woods Hole Oceanographic Institution for 1940 that did not appear in *Papers in Physical Oceanography and Meteorology*. The 33 papers are unrelated to each other. Mostly they deal with the physics and chemistry of sea water, although ecology, taxonomy, and experimentation are not neglected. There is one paper dealing with the flight of birds. The annual report of the Institution is appended.



PROCEEDINGS OF THE SIXTH PACIFIC CONGRESS OF THE PACIFIC SCIENCE ASSOCIATION Held at the University of California, Berkeley, Stanford University, and San Francisco, July 24th to August 12th, 1939. Volume III.

Pacific Science Association. University of California Press, Berkeley and Los Angeles. \$3.50. 9½ x 6; viii + 754; 1940 (paper).

This large volume consists of many contributions on all phases of marine study. Currents, oceanography, distribution of fish, research programs, climatology, are but some of the topics. These studies have all been made on the Pacific Ocean, from east to west.



EL MAR *Acuario del Mundo.*

By Enrique Rioja. Editorial Seneca, Mexico City. \$2.50. 7½ x 5½; 405; 1941.

In this book the author, a well-known Spanish student of animal life of the sea and now pursuing his research in the Biological Institute of the National University of Mexico, writes in a popular style of some of the lower plant and animal forms, coral, mother-of-pearl, fish with protective coloration or chameleon-like characteristics, and monsters, real and imaginary, of the sea. The book is written with authority as well as charm and is profusely illustrated.

MANUAL OF BIOLOGY. Sixth Edition.

By George Alfred Baisell. The Macmillan Company, New York. \$2.75. 8½ x 5½; ix + 449; 1941.

This standard biology text has enjoyed wide popularity and use through five previous editions. The present edition maintains the same high quality of workmanship exhibited by the earlier editions, and with few minor exceptions presents the same well-selected material in the same logical sequence as it appeared previously.



UNIVERSITY OF COLORADO STUDIES. Series D. Physical and Biological Sciences, Vol. I, No. 3. Containing the Following Articles: Keys for the Identification of Colorado Orthoptera, by Gordon Alexander; Effect of X-radiation upon the Growth of *Lemna minor*, by Edna Louise Johnson; Abbreviation of Names of Biological Publications, by Edward D. Crabb; Distribution Problems in Some Moraine Ponds, by Hugo G. Rodeck; An Introduction to the Limnology of Northern Colorado, by Robert W. Pennak; An Anomalous Everted Piece of Ileum in an Adult Cottontail Rabbit, by Edward D. Crabb and Margaret A. Kelsall; A Bibliography of High Altitude Limnological Investigations in the Western United States, by Robert W. Pennak.

University of Colorado, Boulder, Colorado. \$1.00. 10 x 6½; 229; 1941 (paper).



HUMAN BIOLOGY

***THROUGH CHINA'S WALL.**

By Graham Peck. Houghton Mifflin Company, Boston. \$3.50. 9½ x 5½; 371; 1940.

The author visited China for the express purpose of making portraits of the natives and sketching their countryside. The numerous drawings in the book were not put there to illustrate the text; rather the text was written as a commentary on the illustrations.

Peck explains that the disdain which the Chinese feel toward the Mongolian barbarians that are penetrating the frontier is equalled only by that which the barbarians feel for the Chinese. The author is equally interested in both, especially in their personal sanitation, or lack of it, a subject of which he never tires. This interest is always in the individual, never in the group. The individuals also took a great deal of interest in him, and used to assemble outside his window to make peepholes in the paper window pane, that they might witness his ablutions and admire the hair on his body, which they mistook for feathers (the Mongolians have no hair except on the head).

The last few chapters are taken up with the author's experience as a stretcher bearer and ambulance driver for the Red Cross after the actual outbreak of hos-

tilities. The account of the rescue of a fifteen-year-old boy who had been lying in the mud for a month, unprotected from the weather, with a shattered arm hanging limply from the shoulder blade, and a fly-blown and maggot-ridden leg and whose only sustenance had been what he could beg from the peasants who continued to cultivate their rice patches amid the filth and stench of the bodies of horses and human beings rotting together, should be effective in teaching the reader what war means.

But somehow one reads between the lines that even this war will pass. There have been wars in China before, but Chinese civilization has endured for three millenia and after each war it has rolled back again like the rock of Sisyphus. The war may realign all the ephemeral boundaries of Europe, it may destroy democracy and religion in the occident, it may be the tocsin of western civilization, but when it is over the author expects to see the old order in China restored, and when that occurs he is going back again.



♦ RIVER OF RUINS.

By Louis J. Halle, Jr. *Henry Holt and Company, New York.* \$3.00. 8½ x 5½; xii + 334 + 16 plates; 1941.

The unofficial expedition made by the author and a companion to the lesser explored sites of Mayan civilization in Petén, a jungle district lying partly in Mexico and partly in Guatemala, is the subject of this fascinating book. The journey was made mostly by the water routes of the rivers de la Pasión and Usumacinta. At Paso Subín the two explorers felt that they had left the outposts of present civilization. At La Libertad they divided their time between studying the ruins at two sites and an embarrassing attempt to collect bird specimens for the Harvard Museum—their only ornithological venture of the trip. At Tikal and Palenque, the eastern and western extremities, approximately, of the region explored, they found "architectural capitals" from two periods of Mayan civilization. Tikal is considered to have been the first of the cities constructed by the mature Mayan civilization; Palenque the last. Of the well-preserved sculptures on the lintels of the bat-infested temple at Yaxchilán the author writes:

I suppose these stones were designed chiefly to inspire awe, because even across all the barriers to understanding that separate us from them, they have that effect. . . . This is High Mass in any language and in any time, whatever gods it may represent. . . . All this elaboration of costume, all this wealth of artistry, the subtlety of the modeling and the devoted rendering of every detail, were designed to lift men above their common selves to the level of their common aspirations. There is more here than can be measured by any arithmetic—more than what is included in any archaeological report.

In addition to the descriptions of the ruins the book is colored by vivid descriptions of the geography, the natives and "foreigners," the vegetation, animal and insect life of the region, and numerous accounts of the explorers' adventures and misadventures.



♦ TWENTIETH CENTURY INDIANS.

Photographs and Text by Frances Cooke Macgregor with a Foreword by Clark Wissler. G. P. Putnam's Sons, New York. \$3.00. 11 x 8½; xv + 127; 1941.

The stated purpose of this beautifully illustrated volume is to dispel the many vagaries and misconceptions concerning the Indians of the United States. The past century has witnessed the futile attempt on the part of the government and of the people of the United States to destroy the American Indians' native cultural, social, economic, and religious structures, and replace them with so-called "civilized" philosophies, concepts and activities. The fact that the aboriginal populations failed to successfully attain the desired measure of "civilization," and that their stocks were being rapidly depleted, seemed ample reason to believe that the Indians represented an inferior race, and that there was not much hope for them in the present world of competition.

A more recent and hopeful attitude toward the Indian accepts his culture and industry as valuable in themselves without regard to civilized culture and industry. This attitude has resulted in better methods of education and in better health and living conditions for the Indians, and these in turn are preparing them for happier and more successful lives, not as white men, but as Indians.

The author's photographic artistry has contributed greatly to the excellence of the volume. Two maps, one at the beginning and one at the end of the book, are of much interest. The first gives the habitats of the important Indian tribes at the time Columbus discovered America. The total number of Indians at that time has been estimated to be about 846,000. The second map gives the distribution of the principal Indian tribes in the United States today and marks the locations of small communities (Rancherias) in California and (Colonies) in Nevada.



♦ CRIME AND ITS TREATMENT. *Social and Legal Aspects of Criminology.*

By Arthur E. Wood and John B. Waite. *American Book Company, New York.* \$3.50. 8½ x 5½; ix + 742; 1941.

As the sub-title indicates this heavy tome deals with two aspects of criminology, the sociological and the

legal. The latter is discussed in the second half of the volume wherein an informative and comprehensive account is given of the elements of criminal law and of penology—liability, evidence, trial procedures, prison systems, and corrective treatments. Thus, the complete picture is made available of the reactions of our society to the trespassing against its regulations. The supposed cause of this trespassing, i.e. crime, constitutes the substance of the first part of the book. Woods, who is responsible for this part, examines first crime statistics and their value and the case history method of study of crime. He emphasizes the unreliability of crime statistics, and in general has a low opinion of statistical handling of criminological data. So far as the etiology of crime is concerned, the author is mainly interested in the effects of the environment, although a short chapter covers briefly certain aspects of the psychopathology of crime. If this chapter had not been included one could well assume that views on criminality have not made much progress during the last century. Sociologists often accuse the human biologist of lack of appreciation of the so-called social sciences yet the ineffectiveness exhibited by the narrow viewpoint which emanates from the dominating sociological approach should encourage further experimentations along other lines. After all, crime is a behavior problem and man's behavior is rooted in his "lowly nature" as Darwin put it. A selected bibliography follows each chapter and many references are given in the text.



CULTURE ELEMENT DISTRIBUTIONS: XIII. NEVADA SHOSHONE. *Anthropological Records, Volume 4, Number 2.*

By Julian Steward. *University of California Press, Berkeley.* \$1.50. 11 x 8½; v + 151; 1941 (paper).

CULTURE ELEMENT DISTRIBUTIONS: XIV. NORTHERN PAIUTE. *Anthropological Records, Volume 4, Number 3.*

By Omer C. Stewart. *University of California Press, Berkeley.* 75 cents. 11 x 8½; iii + 85; 1941 (paper).

These studies give extensive data, arranged in notes and in tabular form, on the distribution of cultural elements in Nevada Shoshone and the neighboring Northern Paiute. The habitat of the Northern Paiute is uniformly desert, although modified somewhat by streams from the mountain area. The Shoshoneans, dwelling in the region east of the Northern Paiute, occupy an extremely infertile area, which necessarily has had an important effect upon many of their activities. Their food is largely rodents and seeds, which grow widely scattered.

In summarizing and synthesizing the Shoshonean data, uniformity is shown to be greatest in the essential economic traits, such as hunting and seed-gathering: greatest variation in hunting, as in food-

gathering, is in details which are dispensable to the main activity. Shamanism also has general stability. "Its secondary features such as the particular spirits and powers, ritual equipment and behavior patterns, are more variable."

Both of these studies represent careful detailed work and form valuable additions to cultural investigations on Indian tribes in or near the Great Basin.



* SCIENTIFIC ASPECTS OF THE RACE PROBLEM.

By H. S. Jennings, Charles A. Berger, Dom Thomas Verner Moore, Aleš Hrdlička, Robert H. Lowie, and Otto Klineberg. With a Preface by His Excellency Bishop Joseph W. Corrigan. *The Catholic University of America Press, Washington, D. C. Longmans, Green and Co., London, New York, and Toronto.* \$3.00. 8½ x 5½; ix + 302; 1941.

To date it has been unavailing for students of anthropology, sociology, etc. to point out the fallacies of the pronouncements on race superiority or inferiority. The general public is willing to concede that the *others* are not superior to *us*, but no one will accept the verdict that *we* are not superior to the *others*. The latest attempt to present an objective discussion of the race question is constituted by this book. Although it is interesting and contains the writings of eminent men, its effectiveness to influence public opinion must be doubted. One reason is that, with but two exceptions, none of the authors actually deals directly with the main theme. Jennings provides an excellent summary of genetics, Berger discusses briefly the inheritance of psychological traits, Moore presents a learned survey of animal psychology investigations, Hrdlička outlines a classification of races, but only Lowie and Klineberg occupy themselves with the variation of certain traits among racial or national groups. Lowie examines and compares the cultural achievements and moral conduct of certain primitive groups, while Klineberg considers critically the results of intelligence tests made on several national groups. All the articles are praiseworthy but the last two are the only ones which seem pertinent to the theme of the symposium.



* THE COLOUR BAR IN EAST AFRICA.

By Norman Leys. *The Hogarth Press, London.* 7s. 6d. 8½ x 5½; 160; 1941.

That the Nazis are not the only offenders in the application of the philosophy of racial superiority in favor of their own people is well brought out in this book. It traces the history of the settlement of British East Africa, especially the two Rhodesias and Kenya, and the development of laws regulating property ownership, labor, taxation, and education. In the author's

opinion the domination of the British minority is founded on the laws and regulations which tend to discriminate against the African. These regulations limit the independent economic opportunities of the natives and at the same time give educational, social, and political privileges to the white minority.

This disparity [in educational opportunities] is defended on the ground of prestige, because at all cost the rise of a class of "poor whites" must be prevented. That means that a secure position in the ruling caste must be found for the stupidest man of European descent, but no place above the servile for the most gifted African.

Ley reinforces his arguments by a generous use of references and citations on the effects of the "colour bar" in the conduct of agricultural and mining industries and on the daily lives of the people. This is a thought-provoking treatise, whether or not the reader will agree with the author's viewpoint and suggestions for a solution of the problem.



ESKIMOLAND SPEAKS.

By William B. Van Valin. *The Caxton Printers, Caldwell, Idaho.* \$3.50. 9 x 5½; 242; 1941.

In his seven years of missionary and educational work in Alaska, the author of this fascinating volume absorbed much of the psychology, industry, and humanity of the Eskimos. Of no less interest to him was the beauty of the barren arctic wastes, the colorful panorama of the midnight sun, and the magnificent eeriness of the aurora borealis.

As with all other white visitors, explorers, or missionaries in the arctic, the writer is left amazed as well as awe inspired at the success with which life in the arctic (both human and infra-human) wrings from the brutal grasp of eternal winter the necessities for its sustenance. The Eskimos' ability to survive in such an adverse environment combines the keenness of the modern scientist, the foresight of the successful economist, and the stamina of the well-trained athlete.

For those interested in polar life, this book will prove as thrilling as it is informative.



THE SOCIAL RELATIONS OF SCIENCE.

By J. G. Crowther. *The Macmillan Company, New York.* \$3.50. 8½ x 5½; xiii + 665; 1941.

This book is an ambitious undertaking in which the author attempts to survey the scientific activities of man in prehistoric, classical, medieval, and modern times, in order to discover what social conditions are essential for the birth and growth of science. Science is regarded as a social product and the present-day need for an effective social policy for science is stressed.

The material of the first two thirds of the book is essentially a descriptive historical formulation along conventional lines, with emphasis on the interdependence of social and scientific development. The last third of the book is devoted to a description of the distribution of present-day research facilities and a discussion of the social responsibilities of scientists. The style is somewhat didactic throughout. References are given at the end of each chapter and there is an index.



EAST AFRICA.

By Elspeth Huxley. *William Collins, London.* 3s. 6d. 8½ x 6½; 48; 1941.

This little volume by one who has had a long first-hand knowledge of East Africa makes interesting reading. It belongs in The British Commonwealth Series, a group of books designed to contribute to a better understanding of Great Britain and the British Commonwealth. The 12 colored plates of scenic views and 17 black and white illustrations of native life are well done, considering the low cost of the book. In the text Mrs. Huxley gives a clear picture of the many contrasting races to be found in this great region under British rule, where there are such wide divergences in religion, custom, and tradition, outlines the problems which the British Government has had to face in governing these people, and the manner in which these problems are being solved. Those familiar with the author's *White Man's Country* will regret that the volume is so brief.



THE STUDY OF MAN. *University of Pennsylvania Bicentennial Conference, M-B.*

By Lawrence J. Henderson. *University of Pennsylvania Press, Philadelphia.* 25 cents. 9 x 6; 22; 1941 (paper).



ZOOLOGY

BIBLIOGRAPHIA PRIMATOLOGICA; *A Classified Bibliography of Primates Other Than Man. Part I. Anatomy, Embryology and Quantitative Morphology; Physiology, Pharmacology and Psychobiology; Primate Phylogeny and Miscellanea.*

By Theodore C. Ruch. *With an Introduction by John F. Fulton. Charles C Thomas, Springfield, Illinois.* \$8.50. 10½ x 7½; xxvii + 241; 1941.

Serious scientific study of man's nearest animal relations, the lemurs, monkeys, and apes, has for a long time been sadly neglected. In the last few decades, however, rapid progress has been made, resulting in

the young and promising science of primatology. The accumulated knowledge in this important speciality is represented by the 4630 titles of morphological and physiological papers which have been painstakingly collected and classified in the present volume. A future, second part of this monographic bibliography will deal with pathological and taxonomic studies on primates.

In many branches of modern biology and medicine our simian cousins are rapidly replacing laboratory rodents and carnivores as experimental animals, a fact that is directly responsible for a large share in the tremendous recent increase in primatological literature.

This scholarly bibliography is indispensable to all newcomers in primatology and will be particularly helpful in preventing repetition of work that has already been accomplished. The author has faithfully indicated under each title precisely which species of primates has been dealt with. This alone should tend to eradicate that still prevalent and harmful habit, chiefly of medical writers, in stating: "in the monkey I found such and such a condition." With some 600 different species of recent primates and with at times far greater differences between some monkeys and others than between some and man, it is utterly useless to record any observation on "a monkey" without giving species, sex, and age.

The carefully considered and detailed subdivisions of this bibliography are grouped under the major headings of anatomy, embryology, quantitative morphology, physiology, pharmacology, psychobiology, phylogeny, and "miscellaneous". Biology and medicine have been rendered a great service with this unique, practical, and excellently printed volume which forms a very essential part of a safe foundation on which to build in the future.



A FIELD GUIDE TO WESTERN BIRDS.

By Roger T. Peterson. Houghton Mifflin Company, Boston. \$2.75. 7½ x 4½; xviii + 240; 1941.

Most bird students already know Peterson's *Field Guide to the Birds*. The present volume is its counterpart for the western birds. Like its predecessor the object of the book is to enable the student to make field identifications of the birds by characteristic color patterns known as "field marks". To this end, the field marks are given emphasis in the illustrations. One must possess some knowledge as to the families of birds, but after this has been mastered, the descriptions point out the essential features for the identification of the species.

Practically all species considered are illustrated, in part or in whole, either in black or white, or in color whenever the latter is more important than pattern for identification. The descriptions are further en-

hanced by the inclusion of ranges of the species and the song of the bird whenever this feature is helpful, as in some of the flycatchers. It is to be regretted that the plates in many cases are not to be found close to the textual material. For instance, the plate of flycatchers is among the woodpecker descriptions and vice versa. Western fauna is very diversified and the number of geographic races is greater than in the East. The writer was hard put to meet this obstacle, but finally decided to list these forms in an appendix. In the few cases that the races can be separated in the field, the distinguishing characters are given in the text.

There is no doubt that this handy pocket (overcoat size) guide will find as enthusiastic welcome in the West as the former book did in the East. Both together will identify birds anywhere in the United States.



ANIMAL BIOLOGY. Third Edition.

By Michael F. Guyer. Harper and Brothers, New York and London. \$3.75. 9½ x 6; xix + 723; 1941.

This text has been one of the leaders in its field for a decade. The new edition (cf. Q. R. B., Vol. 7, p. 361 and Vol. 12, p. 472 for mention of earlier editions) involves a number of changes designed to increase its usefulness. Numerous sections of the book have been rewritten, some condensed, and others expanded. New material presented includes a very important chapter on ecology, which provides the student with a concise review of the field, an account of the life and structure of planarians, a discussion of ameboid locomotion, and reviews of recent experimental work, especially that on "mating types" in *Paramecium*. In addition, the section on birds has been rewritten, and the classification of mammals reorganized. A number of new illustrations have been added. The author presents the principles of biology in such a way as to retain the value of the usual "types" course, but the emphasis is upon fundamental concepts underlying all life phenomena. The well-chosen, clearly-labelled illustrations are a feature of the book. The volume is concluded with a list of reference books, a glossary, and a complete index.



RETURN TO THE RIVER: A Story of the Chinook Run.

By Roderick L. Haig-Brown. Illustrations by Charles DeFeo. William Morrow and Company, New York. \$3.00. Limited edition, autographed by author and illustrator, \$10.00. 8½ x 5½; 248; 1941.

This is the fascinating story of Spring, a Chinook salmon. It tells of her birth, her travels from the

Grand Coulee region to Puget Sound and the Pacific waters beyond, and her return at the age of five years to spawn and die in the same stream where she was born. Haig-Brown, a British-Canadian ichthyologist and author of the sourcebook *The Western Angler* tells the story of the life-cycle of the salmon in the vein of a novel, but without deviating from facts. The reflections of the old Senator, who was a witness of Spring's birth and death, offer sidelights on the salmon industry and on the use and misuse of natural resources, and conjectures on the possible effects of the completion of the Columbia River dam projects on the survival of the salmon in the Northwest. The illustrations by Charles DeFeo are unusually fine and a fitting accompaniment to the narrative.



WATCHING BIRDS.

By James Fisher. Penguin Books, Harmondsworth, Middlesex, England; Penguin Books, Inc., New York. 25 cents. 7½ x 4½; 192; 1940 (paper).

A bird's eye view of the field of ornithology, its problems, and its methods of study are contained in this little book. After introductory chapters to the class Aves, there follow chapters on migration, on the numbers of birds, their habitats, their territory and breeding cycles, and their behavior. Although it would be impossible to treat all these subjects thoroughly in such a small amount of space, the review has been ably presented for the beginner. Since the writer is British most of the examples are taken from British birds, but the principles are the same for birds of any area.



INSECTS AND THEIR STORIES.

By Harry Hoogstraal. With Camera Studies by Melvin Martinson and Drawings by Carl O. Mohr. Thomas Y. Crowell Company, New York. \$2.00. 7½ x 9½; 144; 1941.

In this fascinating little volume are recorded, in language understandable to the high school freshman, the stories of some 50 of our common house, garden, and forest insects. The stories include observations on the everyday activities, the favorite haunts, the methods of resisting natural forces, and the methods of replenishing the races of both land and aquatic forms.

The excellent photographic work of Martinson adds considerably to the interest and value of the book for budding naturalists. The volume is well indexed. An additional index and guide to the recognition of insects, arranged according to orders, is provided.

BUTTERFLIES. *A Handbook of the Butterflies of the United States, Complete for the Region North of the Potomac and Ohio Rivers and East of the Dakotas.*

By Ralph W. Macy and Harold H. Shepard. The University of Minnesota Press, Minneapolis. \$3.00. 9 x 6; vii + 247; 1941.

The fact that no key to the Lepidoptera of the north-eastern United States has appeared since 1889 is ample reason for the preparation of this excellent work. In addition to the key to 162 species of Lepidoptera, the present treatise includes many interesting details relating to the natural history, distribution, and economic importance of many of our northeastern forms. The volume is beautifully illustrated with both monochrome and dichrome photographs. The description of each species begins with a list of publications relating particularly to that species. A complete index is appended.



STUDIES ON GREGARINA BLATTARUM WITH PARTICULAR REFERENCE TO THE CHROMOSOME CYCLE. *Illinois Biological Monographs, Volume XVIII, Number 2.*

By Victor Sprague. The University of Illinois Press, Urbana, Illinois. \$1.00. 10½ x 7; 144 + 6 plates; 1941 (paper).

The present investigation deals principally with the period that involves syngamy and the meiotic phenomena of this most common and widely known of the Sporozoa. It also includes an account of the process of encystment and the development of the cyst. Five excellent plates and several figures elucidate the text.



STUDIES OF THE NEOTROPICAL COLUBRINAE. VIII. A Revision of the Genus *Dryadophis* Stuart, 1939. *Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 49.*

By L. C. Stuart. University of Michigan Press, Ann Arbor. \$1.15. 10 x 6½; 106 + 4 plates; 1941 (paper).

A CONTRIBUTION TO THE KNOWLEDGE OF VARIATION IN *OPHEODRYS VERNALIS* (HARLAN), with the Description of a New Subspecies. *Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 50.*

By Arnold B. Grobman. University of Michigan Press, Ann Arbor. 35 cents. 10 x 6½; 38; 1941 (paper).

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY. Vol. 43, No. 14. *Studies of Some Amoebae from a Termite of the Genus *Cubitermes, by Joseph C. Henderson.**

University of California Press, Berkeley. 25 cents. 10½ x 6½; 13 + 3 plates; 1941 (paper).

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY.

Vol. 45, No. 1. *Devescovichid Flagellates of Termites*.
I. *The Genus Devescovicha*, by Harold Kirby.

University of California Press, Berkeley. \$1.25.
10½ x 6½; 71 + 9 plates; 1941 (paper).

INDEX CATALOGUE OF MEDICAL AND VETERINARY
ZOOLOGY. Part 5. Authors: E to FYNNEY. U. S.
Department of Agriculture.

By Albert Hassall, Mildred A. Doss, Ruth M. Taylor,
Gertrude B. Carson, and Dorothy B. Segal. Govern-
ment Printing Office, Washington. 45 cents. 9½ x
5½; 1177-1458; 1941 (paper).



BOTANY

FLOWERS AND FLOWERING PLANTS. *An Introduction
to the Nature and Work of Flowers and the Classification
of Flowering Plants. Second Edition.*

By Raymond J. Pool. McGraw-Hill Book Co.,
New York and London. \$3.50. 9 x 5½; xxiii + 428;
1941.

The merited success of the first edition of this excellent
text over the past twelve years has resulted in the
issue of a second edition.

The basic principle on which the entire book rests is
the recognition of the plant as a living, working mech-
anism. The work deals almost entirely with the
taxonomic aspect of botany, and in line with this,
emphasizes the family as the important unit in classi-
fication. The formula method in depicting the promi-
nent floral features of the various families in the master
chart (to which the key constantly refers) is known as
the Besseyan system, and was originated by the author's
former professor, the late Charles Edwin Bessey. While
the main features of the present edition follow
closely those of the earlier work, the present does
include several notable changes. An entirely new
chapter on the vegetative characteristics of flowering
plants has been added, and changes throughout the
text have been made to include the recent work in
plant taxonomy.

The text and key are well supplied with charts
and illustrative material, both graphic and photo-
graphic. Several concluding chapters deal with the
history of plant taxonomy, and the collecting, preserv-
ing, and mounting of herbarium specimens. A final
chapter of reference books, monographs, manuals,
and floras, a glossary, and an index conclude the
volume.



THE REDWOODS OF COAST AND SIERRA. *Second
Edition (Revised).*

By James Clifford Shirley. University of California
Press, Berkeley. \$1.25. 9½ x 6½; 84; 1940 (board).

The first edition of this work appeared in 1937 (cf.
Q. R. B., Vol. 12, p. 115). The revision does not
markedly differ from the earlier version. It suffers
from a peculiar diffuseness of style, so that there is a
good deal of repetition. Also, since the first edition
appeared, the claim of the Sequoias to be the oldest
living things has been seriously challenged twice by
organisms of much humbler appearance—the cycads
of New Zealand and certain single-celled plants ob-
tained from the interior of rocks of geological age.
Both of these seem to be entitled to the same serious
consideration that the author gives to certain other
long-lived plants that are not especially closely re-
lated to the redwoods. Also, the claim to have the
greatest diameter of any tree in the world has been
made on behalf of the chestnut "Tree of One Hundred
Horses" near Catania, which is associated with Napo-
leon Bonaparte. And in 1909 the *National Geographic
Magazine* published a photograph of a *Eucalyptus*
with a diameter of 67 feet, and another still larger.
Exaggerated statements as to the height of Australian
eucalyptus trees may be safely discounted, but it is
difficult to explain away a photograph. The reader
of the work now under discussion is likely to be disap-
pointed by the absence of any reference to these trees.

Of course, in a book as brief as this one it is obviously
impossible to include enough material to satisfy all
readers. The author has assembled a great deal of
information not readily available elsewhere, and his
product is worthy of all the praise bestowed upon it in
these columns when the first edition appeared.



TEXTBOOK OF BACTERIOLOGY. *Thirteenth Edition, Re-
vised.*

By Edwin O. Jordan and William Burrows. W. B.
Saunders Company, Philadelphia and London.
\$6.00. 9½ x 5½; xii + 731; 1941.

The success of the earlier editions of this standard
textbook have established its worth in the scientific
field. The present volume is, with minor exceptions
completely rewritten and is constructed upon a some-
what different basis than its predecessors. The most
obvious manifestation of this change is the elimination
of chapters devoted to the highly specialized applied
fields, such as soil, industrial and dairy bacteriology,
and the incorporation of parts of these, together with
other old and much new material, in a lengthy chapter
on bacterial physiology. The relation of bacteria to
disease is also considered in its broad aspects. The
subject of immunity has been completely reorganized
and is considered in two chapters, the first of which
discusses antigens and related material, while the
second is devoted to specific resistance to infectious
disease. Some of the new material in this edition
includes sections on dental caries, the non-sporulating

anaerobic bacilli, the pleuropneumonia-like organisms, the Rickettsiae, and graphical representation of the secular prevalence and seasonal incidence of the more important infectious diseases. The illustrations are well chosen and extremely well reproduced. The book has been carefully and extensively documented and a total of over 1400 references are given as footnotes throughout the volume. A complete index concludes this excellent college and medical school text.



MODERN FRUIT PRODUCTION.

By Joseph Harvey Gourley and Freeman Smith Howlett. *The Macmillan Company, New York.* \$4.50. 9½ x 6½; vii + 579; 1941.

Since orcharding and fruit culture are assuming ever greater importance in American agriculture, it is not strange to find an increase in the number of good texts dealing with the technique and economic importance of fruit growing.

After an introductory chapter on the economic aspects of the fruit industry, the present text leads into a discussion of the fundamentals of physiology, morphology, soils, and chemistry as related to fruit plants and their ability to yield products of fine quantity and quality. Such broad topics as orchard sites and soils, the planning and setting of orchards, fertilizers and manures, pruning and propagation, harvesting, storing and marketing of fruits are discussed in considerable detail, yet free from the technical language which usually limits the use of good texts to the professional man only. An extremely fascinating and informative chapter on the origin and improvement of fruits has been included.

Each chapter lists the literature cited in that chapter, and the volume is concluded by a 12-page detailed index. The work will be of exceptional value in the hands of students of horticulture as well as orchardists.



PRINCIPLES OF MICROBIOLOGY.

By Francis E. Colien and Ethel J. Odegard. *The C. V. Mosby Company, St. Louis.* \$3.00. 8½ x 5½; 444; 1941.

This fine text fully justifies its boast of presenting something new in the field of microbiology. After a preliminary discussion of the history, the important men, materials, and techniques of bacteriology, the important pathogens are discussed from the point of view of what they do, rather than what they are. Emphasis throughout the volume is placed on the importance of bacteriology in nursing and disease prevention, rather than as a subject for specialization. In consequence, the work will find wider use in the hands of student nurses, medical students, and public

health workers, than in those of the specialized bacteriologist.

The text is well supplied with tables, charts, and photographic illustrations (both monochrome and dichrome). A short list of references is appended to each chapter. A catalogue of the methods of preparing the various culture media, a suggested laboratory program including 21 units of work, a glossary, and a complete index conclude the volume. The excellence of the text is still further enhanced by the use of the new eye-tone paper.



THE PLANT WORLD. *A Text in College Botany.*

By Harry J. Fuller. *Henry Holt and Company, New York.* \$3.25. 8½ x 5½; xi + 592; 1941.

The author has prepared this college text primarily for use by students who are registered in elementary botany courses but who do not intend to continue with advanced work. The author believes that the primary objective of such a course, designed for cultural and general educational purposes should be the presentation of the fundamental features of the structure, physiological activities, and reproduction of flowering plants. The textual material is divided into four main parts: the nature of plants and of plant study; the structure and physiology of flowering plants; a general discussion of the plant kingdom, including a very interesting and instructive presentation of plant diseases; and, finally, the distribution of plants in time and space. A summary is placed at the end of each chapter. The excellent illustrations and colored plates are a distinguishing characteristic of the volume. The appendix contains a modern classification of the plant kingdom, a complete glossary, and an index.



PRUNING TREES AND SHRUBS.

By Ephraim P. Felt. *Orange Judd Publishing Co., New York.* \$2.00. 7½ x 5; 237; 1941.

Felt, Director and Chief Entomologist of the Bartlett Tree Research Laboratories, presents in this book the conclusions of years of research and practical experience in the art of pruning trees and shrubs. Working in conformity to the laws of nature, trees and shrubs are adapted by pruning in such a way as to best serve the diverse human needs of present-day living. In clear, non-technical language the author gives the principles of pruning not only shade trees, but fruit trees, nut trees, flowering shrubs and hedges, woody vines, and small fruits, as well. Ninety-three illustrations serve to clarify the text. All through the book the importance of training the tree while young in the way it should grow, is stressed.

A REVISION OF MELANCONIS, PSEUDOVALSA, PROSTHECIUM, AND TITANIA. *University of Michigan Studies: Scientific Series. Volume XIV.*

By Lewis E. Wehmeyer. *University of Michigan Press, Ann Arbor.* \$2.50. 9½ x 6; viii + 161; 1941.

This is a taxonomic study of the genera of fungi given in the above title. For the specialist only.



CONTRIBUTIONS DE L'INSTITUT BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL, No. 32. Contains the following articles: *Sur deux formes nouvelles de Micrasterias*, by Jules Brunel; *Les prothalles de Lycopodes dans le Québec*, by Roger Gauthier and Rolland Dumais; *Notes floristiques sur l'est de la Nouvelle-Écosse*, by Jacques Rousseau.

Institut Botanique de l'Université de Montréal, Montréal. 25 cents. 9 x 6; 62; 1938 (paper).

BIBLIOGRAPHIE DES TRAVAUX BOTANIQUE Contenus dans les "Mémoires et Comptes rendus de la Société Royale du Canada", de 1882 à 1936 inclusivement. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 33.*

By Jacques Rousseau, Marcelle Gauvreau, and Claire Morin. *Institut Botanique de l'Université de Montréal.* 50 cents. 9 x 6; 117; 1939 (paper).

LA FLORULE DE LA GROSSE-ÎLE. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 34.*

By Frère Marie-Victorin and René Meilleur. *Institut Botanique de l'Université de Montréal, Montréal.* 25 cents. 9 x 6; 20; 1940 (paper).

HISTOIRE DE LA NOMENCLATURE DE L'ACER SACCAROPHORUM K. KOCH (A. SACCARUM MARSHALL) DEPUIS 1753. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 35.*

By Jacques Rousseau. *Institut Botanique de l'Université de Montréal, Montréal.* 50 cents. 9 x 6; 66; 1940 (paper).

NOUVELLES ENTITÉS DE LA FLORE PHANÉROGAMIQUE DU CANADA ORIENTAL. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 36.*

By Frère Marie-Victorin and Jacques Rousseau. *Institut Botanique de l'Université de Montréal, Montréal.* 50 cents. 9 x 6; 74; 1940 (paper).



MORPHOLOGY

OPTICAL ACTIVITY AND LIVING MATTER.

By G. F. Gause. *Biodynamica, Normandy, Missouri.* \$2.75. 9½ x 6½; 162; 1941.

This work is a discussion of asymmetry and dyssymmetry. By definition the first of these terms is made to apply to the arrangement of molecules in a structure, and the other to the arrangement of atoms in a mole-

cule. Such structures can not be superimposed on their mirror images, to which they bear a heterostrophic relation. The author's thesis is that in inert substances either form of a heterostrophic pair can occur about as often as the other, but that in living organisms one form will always displace the other. This is reminiscent of a doctrine promulgated sometime ago, that if two species occupy the same niche in the environment one of them will disappear. The theory seems borne out by the author's own experiments, but his bibliography of 21 pages covering over a century of investigation makes no mention of the pioneer work of Gulick on the Achatinellidae which have a different story to tell. Also, it contains only one item from the publications of Boycott, Diver, and their satellites on inverse symmetry.

The work is stimulating, but much more experimentation is needed before the theory can meet with universal acceptance.



FUNDAMENTALS OF COMPARATIVE EMBRYOLOGY OF THE VERTEBRATES.

By Alfred F. Huettner. *The Macmillan Company, New York.* \$4.50. 9½ x 6; xiv + 416; 1941.

It is obvious that the present volume is the product of long years of teaching experience. The clearness and order of the exposition are evidence of it. But, in addition, the author has for the major part provided original illustrations that actually reproduce the objects seen and do not require, as is often the case, a tremendous effort of cerebration and a vivid imagination. The subject matter is contained in 19 chapters of which the first four are devoted to an introduction to the subject, history of embryology, cell structure, and reproduction. A fifth chapter deals briefly with amphioxus. Chapters 6 to 8 describe the embryology of the frog, and chapters 9 to 15 that of the chick. These descriptions are accurate, detailed, and expressed with remarkable simplicity of style and language. The final chapters deal with mammals and man. There is an index but no list of references. Except for this omission, the present textbook satisfies the most exacting requirements. It will undoubtedly prove very popular for college courses.



CYTOLOGY, GENETICS, AND EVOLUTION. *University of Pennsylvania Bicentennial Conference.*

By M. Demerec, Charles W. Metz, Franz Schrader, Albert F. Blakeslee, Th. Dobzhansky, Clarence E. McClung, Herbert S. Jennings, William F. Diller, T. M. Sonneborn, Leon Churney, William R. Duryee, Paul S. Henshaw. *University of Pennsylvania*

Press, Philadelphia. \$2.00. 9 x 6; v + 168; 1941.

This is a collection of papers by twelve of the most eminent biologists of the country. The topics covered concern a variety of approaches, techniques, and problems but all referring to the elements of the cell, their properties, and behavior. Space is not available to review the papers in detail but it is to be remarked that few symposia have produced such an aggregate of stimulating articles as we have here. One does not find the dull reexamination of well-known past accomplishments nor the repetition of textbook statements. The investigators represented are probing deeper into the fundamentals of biology and the student can find no more illuminating record of the advances being made or hoped for than the summary presented in this volume.



HUMAN ANATOMY AND PHYSIOLOGY.

By *Nellie D. Millard and Barry G. King.* *W. B. Saunders Company, Philadelphia.* \$3.00. 7½ x 5½; vii + 525; 1941.

This book has been prepared for the use of nurses and certainly seems to be satisfactory for the purpose. Of course, it is elementary and this is particularly noticeable with reference to the style in which it is written. The exposition of the subject matter follows a rather novel style which deserves to be remarked. A functional approach has been employed. The description of each organ or organ-system is introduced by a discussion of its general functions, then the morphology, and finally the physiology of the structure is dealt with. Thus, the skeletal muscles are described as muscles which move "apart", for example, the femur, and they are arranged in opposing groups; flexors and extensors, adductors and abductors, instead of the usual grouping of muscles of the thigh. Many of the illustrations are original and commendable.



THE PLAGIOSTOME HYPOPHYSIS, *General Morphology and Types of Structure.*

By *Harry W. Norris.* Obtainable from the Author, *Grinnell, Iowa.* 50 cents (paper); \$1.00 (cloth). 10 x 6½; 91; 1941.

The hypophysis of the plagiostome fishes (herein to include all elasmobranch fishes except the Holocephali) has been investigated in this anatomical study. On the basis of 51 genera the writer concludes that the plagiostome hypophysis has no exact detailed homologue in other vertebrates. The lobes of the plagiostome hypophysis, however varied in size, shape, and situation, or in attachments and other relations to brain, saccus vasculosus, and cranial walls, always conform to the

definite plagiostome hypophyseal type. The anterior and interior lobes vary but little from species to species, but the ventral is highly variable in many ways.



CYTOLOGICAL OBSERVATIONS ON *ENDAMOEBA BLATTAE*. *Illinois Biological Monographs, Volume XVII, Number 4.*

By *Paul A. Meglitsch.* *The University of Illinois Press, Urbana.* \$1.00. 10½ x 6½; 147; 1940 (paper). In this study on *Endamoeba blattae*

a comparison of the results proceeding from the use of basic dyes and the Feulgen reaction were made in order to determine the relationship of basophilic material to nucleic acids, as demonstrated by the Feulgen reaction, throughout the life cycle up to the formation of the mature cyst, . . . As a result of the study, in addition to details of nuclear division during the trophic and cystic stages, it has been possible to observe a cyclical variation in the quantity and distribution of nucleic acid, as determined by the Feulgen test, correlated with the processes of nuclear division and encystment. Several unusual relationships between the basophilic material and the nucleic acid-containing material have also been observed.

Eight fine plates (91 figures) and a bibliography conclude this careful study.



THE PRINCIPAL NERVOUS PATHWAYS: *Neurological Charts and Schemas with Explanatory Notes. Second Edition.*

By *Andrew Theodore Rasmussen.* *The Macmillan Company, New York.* \$2.50. 11 x 8½; ix + 73; 1941.

In this second edition of very useful charts of the principal pathways of the nervous system the author has included well-established alterations which investigative work in the field since 1932, the year of the first edition, has contributed. No basic changes in organization of the material or in the form of the charts have been made. The book should continue to prove helpful particularly to medical students.



PHYSIOLOGY AND PATHOLOGY

NATIVE AFRICAN MEDICINE with *Special Reference to its Practice in the Mano Tribe of Liberia.*

By *George Way Harley.* *Harvard University Press, Cambridge, Massachusetts.* \$3.00. 9½ x 6; xvi + 294; 1941.

The author of this work was for many years a medical missionary in Liberia. The training which he received at the Kennedy School gave him an appreciative attitude toward native culture, and a desire to study the

medical practices of the natives from the standpoint of the student of folk-lore, as well as from that of the physician. The present volume is largely the result of his own observations among the medicine men of the Mano tribe, but it also contains a great deal of information about native medical practices throughout Africa, which he acquired from the leading libraries of London during a year of sick leave. While in London he and his wife studied botany, and after returning to Liberia they assembled a herbarium of over 1000 species, of which more than 100 have definite therapeutic value.

The ability of the medicine men to recognize different kinds of diseases is remarkable, and although they know nothing of the functions of the organs in the human body, in a particular case they can generally locate with uncanny accuracy the organ that is ailing. Each illness has its own method of treatment, in which internal medicine, external applications, massage, exercise, and magical incantation play their part. The latter may be the result of superstition but more often it is for the purpose of distracting the attention of onlookers, so that the real treatment and specific medicine may remain the secret of the medicine man. That some of the drugs used are really efficacious the author does not doubt; he cites authentic instances of successful treatment by native witch doctors of cases which the white physicians had abandoned as hopeless.

The knowledge of the correct treatment of specific diseases seems to have been acquired originally by the trial and error method, but today it is learned by joining one of the two great secret societies of Liberia—the Poro for men and the Sande for women. The initiation into these societies is laborious, painful, and expensive. Having paid the price for entry the “zo” cannot afford to let the general public in on his means of gaining a livelihood. To retain the respect and confidence of his clientele, elaborate ritual and even fraud are employed. The author describes treatments, some of them successful, which nevertheless were largely ceremonial. To draw the line between legitimate medicine and ceremonial magic is impossible. The two must be studied together. The ceremonial never injures the patient and the medicine may help, but the use of the blacksmith’s tongs to restore a dislocated jaw bone seems slightly drastic.

An appendix lists over 200 plants believed by the natives to be medically useful. In transliterating the native names the author has had recourse to letters and diacritical marks that do not occur in the English alphabet, and the reader who finds himself confronted by these strange symbols is likely to regret that there is no explanation of their meaning given. Such would improve the book, as would also a few more photographs similar to the lonely frontispiece. There is an index of 16 pages and a bibliography of 7 pages.

SCHOOL HEALTH SERVICES. *A Study of the Programs Developed by the Health Department in Six Tennessee Counties.*

By Frank Walker and Carolina R. Randolph. *The Commonwealth Fund, New York.* \$1.50. 9 x 5½; xi + 172 + 35 tables; 1941.

For years school children all over the country have been receiving physical examinations of one sort or other, but only in a few places have any attempts been made to set up the organization for corrective work. In view of the findings of the selective service examinations the question arises as to the value of school health programs. This monograph provides a bit of information on the point. In Tennessee it is required that school children be examined every two years and apparently in some instances provision has also been made for corrective work—although what the actual arrangements are is not clear from this report. The authors have examined the records of six selected counties to evaluate the effects of the program from 1930 to 1936. The main findings appear to be that twelve-year-old children in 1936 have less decayed teeth and diseased tonsils and better nutrition than the twelve-year-old children seen in 1930. Thus, it is assumed that some benefits have been obtained by the school health program even though with respect to visual defects no change in prevalence is noted. It is particularly significant to learn that only about 33 percent of dental defects, about 4 per cent of throat defects, and 12 per cent of visual defects are corrected after any examination, and that repeated examinations do not apparently increase the frequency of correction. Unfortunately, the data on which the report is based are defective in many respects and, therefore, the value of the findings is considerably limited.



VERHANDLUNGEN DER DEUTSCHEN GESELLSCHAFT FÜR KREISLAUFFORSCHUNG. *XIII. Tagung zu Wiesbaden vom 6. Mai 1940. Hauptthema: Kreislauf und Atmung.*

Edited by Eb. Koch. Theodor Steinkopff, Dresden and Leipzig. RM. 10 (in Germany); RM. 7.50 (outside of Germany). 9½ x 5½; xxxii + 182; 1940 (paper).

References, contributions, and speeches of the German Society for Circulatory Research are embodied in this volume. The opening pages give a statement of the purpose of the association, the proceedings of the previous meeting, and the opening report to the group. In all, there are twenty-two papers presented, with the principal discussions which followed each report. The first gives a general review of studies on circulation and respiration, not as isolated works, but in an effort to combine the various aspects of the two functions into a unified whole. The second paper emphasizes

the clinical applications of studies on circulation and respiration, especially lung collapse therapy. The chemical control of the mutual interrelation between breathing and circulation is then discussed. Some of the more important of the remaining papers concern the clinical aspects of silicosis in its effects on cardiac insufficiency, the effect of anoxemia produced by high altitude flying or experimental low oxygen concentration, lung ventilation and circulatory insufficiency in conjunction with certain related pathological conditions, experimental studies on circulatory collapse due to heart infarction, investigation of peripheral circulation by means of ultra red light, and electrocardiographic studies among twins. Most of the papers contain very good photographs, diagrams, and bibliographies. The volume itself is concluded with an index of authors and subjects.



BLUTDRUCKMESSUNG UND KREISLAUF IN DEN ARTERIEN DES MENSCHEN. *Geschichte und heutige Lage der Probleme neue Lösungsversuche.*

By *Henrich von Recklinghausen. Theodor Steinkopff, Dresden und Leipzig.* RM. 30.00 (outside Germany). 9½ x 6½; xx + 532; 1940 (paper).

The early pages of this volume discuss the historical development of methods used for the measurement and recording of blood pressure and pulse curves. Diagrams of the various types of apparatus are given and results of the observations are critically discussed. Particular attention is paid to the findings upon which the step-curves are built up. Two principal types are described in detail, the pulse amplitude step-curve and the pulse form step-curve. The author next takes up the mathematical and graphic analysis of the pulse wave and the dynamics of arterial circulation, describing at some length the alterations which occur in the various components of the wave as it progresses to different points along the arteries. The significance of these findings for the practical determination of blood pressures by direct and indirect methods, and also the application to certain clinical conditions is thoroughly treated. A fourteen-page summary covers the general information in the text, but proper understanding of such details as the systolic and diastolic criteria can be obtained only by reference to the text itself. Several tables at the end of the volume outline the criteria used by various observers, summarize the mathematical formulae, and show in brief the principal hemodynamic principles. There is an adequate bibliography and a good index.



FAMILY FOOD CONSUMPTION AND DIETARY LEVELS. *Five Regions. U. S. Department of Agriculture,*

Miscellaneous Publication No. 405. Consumer Purchases Study. Farm Series.

By *Hazel K. Stiebeling, Day Monroe, Callie M. Coons, Esther F. Phipard, and Faith Clark. Government Printing Office, Washington.* 35 cents. 9½ x 5½; vi + 393; 1941 (paper).

FAMILY EXPENDITURES FOR HOUSING AND HOUSEHOLD OPERATION. *Five regions. U. S. Department of Agriculture, Miscellaneous Publication No. 432. Consumer Purchases Study. Urban and Village Series.*

By *Hazel Kirk, Day Monroe, Kathryn Cronister, and Margaret Perry. Government Printing Office, Washington.* 25 cents. 9½ x 5½; v + 244; 1941 (paper).

The first of these publications presents information on the food of farm families at different income levels in the 66 counties surveyed. The relationships between income and family composition, consumption of different types of food, and nutritive value of farm family diets are some of the topics discussed.

The second publication, dealing with expenditures for housing and household operation of families living in villages and small cities, but excluding relief groups, foreign-born, one-person and broken families, and Negroes, except in the Southeast where they were studied as a separate population group, gives interesting comparisons between the patterns of the spending of home owners and of renters. Both volumes include the statistical data on which the studies were based.



* FATAL PARTNERS: *War and Disease.*

By *Ralph H. Major. Doubleday, Doran and Company, New York.* \$3.50. 9 x 6; ix + 342; 1941.

The course of history has often been profoundly changed by disease even more than by the outcome of wars. Some of the mightiest armies have fallen before typhoid, typhus, or bubonic plague, and have been scourged by scurvy. For the many centuries during which the sword and spear were the chief weapons and siege the established method of warfare, these diseases were the principal enemies of soldier and civilian alike. Later, progress in medical science largely eliminated the danger of such epidemics, and still more recent advances have almost banished malaria and yellow fever from the causes of fatalities. However, other grave medical problems have arisen consequent upon the use of explosives and mechanization of armies. Major tells a fascinating story of the companions in destruction, disease and war, from the days of the ancient Greeks to the present struggle. No war has been without some advance in medical knowledge, since wars serve as vast laboratories for testing discoveries made during times of peace. Although we still read of typhus in some of the armies of the present conflict, and of trench fever in air raid shelters, the principal problems concern shell shock and treatment of

infections. These, too, are yielding to advances in the study of psychiatry, to rapid ambulance service, and to chemical treatment. "The present war illustrates, more than any other war in the history of the world, that the science of saving life, as well as the science of destroying life, has made great progress."



PAPERS OF WADE HAMPTON FROST, M.D. *A Contribution to Epidemiological Method.*

Edited by Kenneth F. Maxcy. *The Commonwealth Fund, New York.* \$3.00. 9½ x 6; viii + 628; 1941. Wade Hampton Frost was a fine teacher and his precepts have had a tremendous influence on the development of epidemiology in this country. His efforts were never directed towards the elaboration of theories, but, being what might be called a naturalist of crowd diseases, he stressed always the need for accurate observations, simple and logical quantitative analysis, and above all, clear thinking. These attributes are in evidence in all of Frost's writings and particularly in the 20 papers which Maxcy has brought together and briefly discusses. The articles are grouped into five sections. The first two include reports on field investigations in which Frost himself participated at the beginning of his career. The third section includes the papers resulting from the studies on influenza and the common cold. The final two sections contain articles dealing in the main with the methodology of epidemiology. In a sense these are the most interesting inasmuch as they reveal Frost's broad conception of public health problems, an outlook which has not yet been fully appreciated by the profession. A complete bibliography of Frost's writings is appended, and Maxcy has also contributed a short biographical note.



AN INTRODUCTION TO MEDICAL SCIENCE. *Second Edition, Thoroughly Revised.*

By William Boyd. *Lea and Febiger, Philadelphia.* \$3.50. 9½ x 5½; 358; 1941.

Nurses and premedical students often find difficulty in combining their studies of anatomy, bacteriology, physiology, histology, and genetics into an integrated whole. These are often presented as apparently separate subjects, and each is highly complex in itself. This volume (for earlier edition, cf. Q.R.B., Vol. 12, p. 380) demonstrates how the several studies must be considered together for attainment of an adequate understanding of medical problems. The first part deals with the general principles of circulation, inflammation, bacterial infections, parasitism, and natural resistance. The second, and major portion of the book, concerns the pathology of specific diseases presented, by and large, according to organ systems. The closing chapters con-

sider practical application, preventive medicine, and the value of the nurse to the laboratory.

Although the treatment of each section is necessarily brief, it is thoroughly understandable. The small photographs are good, but the drawings are mostly inferior. The volume is well written, fulfills its purpose, and is adequately indexed.



IMMUNITY AGAINST ANIMAL PARASITES.

By James T. Culbertson. *Columbia University Press, New York.* \$3.50. 9 x 6; viii + 274; 1941.

Both the beginning and the more experienced student of immunity to the parasitic forms should welcome this very considerable contribution in a field of investigation not overly burdened with clear and concise published works. Essentially, researches of devious and diverse nature form the material basis of this book. Its value is further enhanced by the predominance of fact everywhere—personal concepts and theories being practically eliminated. The textual material is presented in three parts: (I) Natural resistance and acquired immunity, in which natural and age resistance, requisites for immune response, parasites which elicit immunity, and mechanisms and demonstration of immunity are discussed; (II) Immunity in specific diseases, including the amoebiasis, leishmaniasis, trypanosomiasis, malarial, coccidiosis, trematodiasis, cestodiasis, nematodiasis, and response to arthropods; (III) Applied immunity, describing the classification of and vaccination against parasites, and the diagnosis of parasitic infection. Ably and coherently written, carefully and extensively documented with over 1300 references, completely indexed, and attractively printed, the volume will prove very useful to the beginner, the trained investigator, and the practicing physician and veterinarian alike.



FUNDAMENTALS OF HEALTH: *Its Development and Conservation. Revised Edition.*

By T. Bruce Kirkpatrick and Alfred F. Huettnier with the Collaboration of Clara Mae Taylor. *Ginn and Company, Boston.* \$3.50. 8½ x 5½; ix + 595; 1941.

The material included in the original edition of this text was based upon a systematic survey of the interests and requirements of university students. It was found that the students wanted and needed a knowledge of bodily structure, function, and development as a foundation upon which to build proper health habits and attitudes, and not a mere recitation of hygienic dogmas. After observing the reactions of several thousand students during the past eight years, the writers feel that their original convictions were sound. The present edition incorporates the more recent findings concerning embry-

ology, nutrition, internal secretions, bacteriology, immunology, and public health. As in the original writing, there is a considerable amount of space devoted to the principles of evolution, heredity, development, the function of the various organ systems, and proper health procedures for the maintenance of proper function. The photographs and diagrams are of only average quality, but there is an excellent list of selected readings. The volume contains a glossary and is well indexed.



INFANTILE PARALYSIS. *A Symposium Delivered at Vanderbilt University, April, 1941.*

By the National Foundation for Infantile Paralysis. National Foundation for Infantile Paralysis, Inc., New York. \$1.25. 9 x 6; v + 239; 1941.

This book contains much informative material for physicians and health officers. The six lectures, by well-known specialists, approach the problem from as many different angles and embody all the recent knowledge concerning this disease. It is now recognized that there may be as many strains of poliomyelitis virus as types of pneumococci and that the disease differs in different species of susceptible animals. With the discovery of the virus in feces and sewage, a new lead has been given as to the way in which poliomyelitis is spread. The problem seems to be growing in complexity but it is by no means insoluble, as this survey indicates. In addition to the sections on the history, etiology, immunology and serology, pathology and pathogenesis, and epidemiology of poliomyelitis, there is a chapter on treatment and rehabilitation of the patient which will be extremely useful to physicians and nurses. A bibliography of 575 titles and an index are provided.



THE PARASITES OF MAN IN TEMPERATE CLIMATES.

By Thomas W. M. Cameron. The University of Toronto Press, Toronto. \$3.00. 9 x 5½; xi + 182; 1940.

This work is based on a course of animal parasitology given in the medical school of McGill University. It is intended for the medical man who practises in the English-speaking temperate and sub-tropical zones. Only parasites which actually occur in North America or Great Britain are discussed in detail; those which may be introduced in patients from the tropics, but which cannot become acclimatized, are dealt with as briefly as possible, while odd, aberrant, or doubtful forms are omitted entirely. Since the volume is not designed for the student of tropical medicine or for the parasitologist or laboratory worker, the material has been selected to include only that required by the prac-

itioner. The chapters deal with protozoa, helminths, leeches, and arthropods, with a final chapter on parasitological technique. The bibliography has been reduced to a minimum and only monographic or similar works have been included. The book is enriched by appropriate illustrations and is indexed.



PERSONAL HYGIENE APPLIED. *Seventh Edition, Revised.*

By Jesse Feiring Williams. W. B. Saunders Company, Philadelphia. \$2.50. 7½ x 5½; xvi + 529; 1941.

A college textbook of proven leadership in its field. However, there is no reason why this book should be limited to school or college, since physicians, teachers, nurses, and social workers may safely recommend it to parents or patients in need of guidance for living. Some of the new material in this edition includes an up-to-date consideration of the vitamins, a simplified discussion of infection and immunity, a rewritten chapter on the endocrines, a revised consideration of the safety problem as it relates to the automobile, and a new discussion of human heredity and its effects on the abilities and talents of the individual. The illustrations are especially praiseworthy. Questions and exercises and a list of selected readings are placed at the end of each chapter. The appendix provides a suggested list of topics for a term report, and a typical "true-false" test as given at Columbia University. A comprehensive index concludes this excellent textbook.



THE BODY FUNCTIONS: Physiology.

By Ralph W. Gerard. John Wiley and Sons, New York. Chapman and Hall, London. \$1.75. 8½ x 5½; xiii + 289; 1941.

This book is one of a series (Wendt Science Series) designed to give the reader more than just a superficial survey of the sciences, but at the same time to avoid the burden of technical terms. Part one concerns the effectors and regulators of the body—muscles, nerves, internal secretions—and how they function. The second section deals with circulation, respiration, digestion, excretion, protective mechanisms, and reproduction. The central nervous system and behavior are discussed in the closing chapter. Enough anatomy, histology, and biochemistry are presented throughout the pages to clarify the descriptions of functions, and numerous simple physiological experiments are described, assuring a thorough understanding of the principles involved. Each chapter is concluded with an excellent list of references, and the book contains a complete glossary-index.

THE FURTHERANCE OF MEDICAL RESEARCH.

By Alan Gregg. Yale University Press, New Haven, Oxford University Press, London. \$2.00. 8 x 5½; ix + 129; 1941.

The Director for the Medical Sciences of the Rockefeller Foundation first attempts to define medical research, second to discuss the relations of institutions conducting or furthering medical research with each other—especially the relations between foundations and universities—and third, to give an insight into the qualifications and personality of the individual research worker. It is evident that the author is aware of the points of view of both the donor foundations and the recipient institutions. He gives a provocative discussion of the shortcomings of the present system of foundation organization and the distribution of grants for research purposes in the United States, together with suggestions for improvement. The book is based on the eighteenth series of Terry Lectures delivered at Yale University.

**THE COMPLETE WEIGHT REDUCER.**

By C. J. Gerling. With a Foreword by Winfield Scott Pugh. Harvest House, New York. \$3.00. 8 x 5½; 246; 1941.

This is in the nature of a handbook for the corpulent individual. In it will be found, under headings arranged alphabetically, brief and easily comprehended discussions of types of food, popular diet systems, reducing menus, commercial products, reducing machines, forms of exercise—in fact, very nearly everything that quackery as well as sound investigation has produced for the guidance of those who find themselves with overweighted constitutions. Numerous frauds are exposed. The book is intended only for persons who have no chronic functional or organic disorder, and only for those adults, who, having a moderate degree of overweight, wish to reduce in a rational manner. There is no index to the volume but this is unnecessary with the arrangement of the material in dictionary form.

X-RAY THERAPY OF CHRONIC ARTHRITIS. (*Including the X-ray Diagnosis of the Disease*). Preliminary Report Based on 100 Patients Treated at Quincy, Illinois.

By Karl Goldhamer. With a Foreword by Harold Swanberg. Radiologic Review Publishing Co., Quincy, Illinois. \$2.00. 9 x 5½; 131; 1941.

The chapter headings of this discussion on the x-ray diagnosis and treatment of chronic arthritis are as follows: Clinical aspects and pathology of chronic arthritis; Roentgen findings in chronic arthritis; How do x-rays act in chronic arthritis?; What cases should be treated by x-rays?; Technique of treatment; Report of patients; Results; Conclusions. The author found that "The

results of irradiation were good in almost all forms of chronic arthritis and were startling and decisive in some types." A list of 52 references is given but there is no index.

**BIOCHEMISTRY****ANNUAL REVIEW OF BIOCHEMISTRY. Volume X.**

Edited by James M. Luck and James H. C. Smith. Annual Reviews, Inc., Stanford University P.O., Cal. \$5.00. 8½ x 6; xi + 692; 1941.

The editors call to the reader's attention a serious impact of the war upon the *Review*, namely, the irregularity and delay in the receipt of many journals. "Almost every article in the present volume has been submitted by its author with apologies for the restrictions in content imposed by the unavailability of recent numbers of important journals." Another effect is upon the international character of the *Review*. It is expected, however, that in Volume XI, the international character will be more manifest than in Volume X.

Twenty-four papers make up the volume. All of them are important for the biochemist, but the general biologist will also find a number that are of especial interest to him. The chapter on bioluminescence should not be missed. Others are on plant growth substances, spectrometric studies in relation to biology, mineral nutrition of plants, relation of soil and plant deficiencies and of toxic constituents in soils to animal nutrition. The two longest reviews are on hormones (52 pages) and water-soluble vitamins (48 pages). As is the custom, all papers are documented and the volume concludes with author and subject indexes. In the autumn of 1941 a cumulative author and subject index to Volumes I to X was published. Those possessing a full set of this valuable series are indeed fortunate.

OUT OF THE TEST TUBE. Third Edition Revised and Expanded.

By Harry M. Holmes. Emerson Books, Inc., New York. \$3.00. 9 x 6; 305; 1941.

To the average intelligent layman, the field of chemistry represents one of the most appealing and revealing of all the subjects under investigation by modern scientific man. The present volume (cf. Q. R. B., Vol. 12, p. 495 for earlier edition) makes a very real and very definite contribution to the chemical education of the general reader. This excellent popularization represents the efforts of an expert in writing a simple, straightforward, and up-to-date account of the marvels of chemistry and the effect of these on our everyday lives. A few of the more interesting of the forty-odd chapters are concerned with: the importance of high vacua; hydrogen—the lightest substance known; oxygen—the elixir of life;

chemical warfare; atom smashing; silks and cellulose; fuels and smoke; chemistry and the motor car; chemistry of foods and nutrition; chaining the sun; the chemist in crime detection; the farm as a factory; what transportation owes to the chemist; minerals and world power; and the house of the future. The concluding chapter on strategic raw material is especially timely. The book is indexed and contains over one hundred striking illustrations. It is heartily recommended to all those who have an acute and healthy interest in the life of modern man and who wish to keep abreast of the contributions of chemical science to the comfort and convenience of living in the twentieth century.



POLAROGRAPHY. *Polarographic Analysis and Voltammetry. Amperometric Titrations.*

By I. M. Kolthoff and J. J. Lingane. *Interscience Publishers, New York.* \$6.00. 9 x 5½; xvi + 510; 1941.

A presentation of a thorough and critical assay of the theory, then of the practice, of the polarographic analytical method so far developed. The delicacy, extreme range, and the automatic nature of the method available make it of great value for all analysts—inorganic, organic, or biological. To be used, polarographic analysis must be well understood. The present volume goes far in its effort to explain the “ins and outs.” Following this explanatory part, detailed methods of analysis are presented for many elements—complex salts, organic radicals and compounds, cancer tissues, etc. An important part of the text is the critical review of the literature through December, 1940. The appendix, which contains a table of potentials of common reference electrodes, and one of half-wave potentials of inorganic substances, and a chart of half-wave potentials of common inorganic substances in various supporting electrolytes, can be purchased separately. Author and subject indexes conclude the volume.



PLANT GROWTH SUBSTANCES. *Their Chemistry and Applications, with Special Reference to Synthetics. Second Edition, Revised.*

By Hugh Nicol. *Chemical Publishing Company, Brooklyn, N. Y.* \$2.00. 8½ x 5½; xii + 148; 1941. The first edition of this book was devoted almost entirely to the chemistry of substances, mainly synthetic, that produce, control, or regulate the growth of plants. Some physiological aspects are included in the present edition. When the book was first published the principal application of synthetic substances had related almost entirely to the treatment of cuttings. Recent

work in the treatment of seeds and in grafting has now been included. Although the vitamins B (thiamin) and C (ascorbic acid) have been discovered to be potent growth regulating substances when applied to plants, there is little discussion concerning these except by indication of the most important studies. Rather, more attention is devoted to the less publicized indole and naphthyl compounds. Author and subject indices are provided.



DIE METHODEN DER FERMENTFORSCHUNG. Lieferung 8.

Edited by Eugen Bamman and Karl Myrbäck. *Georg Thieme Verlag, Leipzig.* R. M. 34.50 (outside of Germany). 11 x 8; 2589–3047; 1941 (paper).

This is the last volume, with the exception of the bibliography which will appear separately, of the important series on biological compounds, and techniques and methods applicable to enzyme investigation. In it are described the distribution, purification, properties, and actions of aspartase, peroxydase, katalase, hydrogenase, catalytic systems of unknown actions such as RSSR—RSH, ascorbic acid, and quinonoids. CO₂ assimilation by green plants and certain bacteria, N₂ assimilation, antienzymes and various models of enzyme action are also discussed. The latter part of the volume deals with enzymes important to industry and to the clinic (in particular, those apparently specific in carcinomas), the trends of future work along these lines, and the productive fields which enzyme research is opening up.



AN INTRODUCTION TO ORGANIC CHEMISTRY. Fourth Edition.

By Roger J. Williams. *D. Van Nostrand Company.* \$4.00. 8½ x 5½; xiii + 628; 1941.

With justifiable pride the author points (in his preface) to the characteristics which have made this textbook so popular that it has gone through four editions and nine reprintings since 1927. Among the main features of the book is its logical exposition with emphasis on the relationship between organic and inorganic chemistry. For example, the ethers, esters, acyl halides, etc. are conceived and described as belonging to a group of acidic anhydrides with fundamental properties in common. In this revision the necessary additions consequent to recent discoveries have been made, but on the whole the contents and style of exposition are the same as those of the previous editions. There can be no doubt that the book will retain its high position as a college textbook.

SEX

CLINICAL AND EXPERIMENTAL INVESTIGATIONS ON THE GENITAL FUNCTIONS AND THEIR HORMONAL REGULATION.

By Bernhard Zondek. *The Williams & Wilkins Co., Baltimore.* \$4.50. 9 x 5½; xxiv + 264; 1941.

In this volume are brought together a series of reports on the author's work in Palestine since 1935. The investigations have covered a wide field but the results are all of interest to the general biologist as well as to the endocrinologist. There is a report on the occurrence of some extrogenic substances in nature—in the waters of the Dead Sea, among other places. The problems studied may be classed under two general groups. The first deals with the effects of the administration of extrogenic and androgenic hormones. Experiments and observations are reported with reference to the percutaneous application of the hormones—the morphological and physiological changes produced by the duration of the administration of the substances in varied dosages. The second group of studies contains the findings related to the menstrual cycle and its mechanism. The author outlines his hypothesis on the mechanism of menstruation which in his view is produced "by harmonious action of the gonadotropic and ovarian hormones independently of the ovum." Much of the work summarized here is already known but the value of this volume is not diminished thereby, particularly since the author has attempted to integrate his own and the findings of others. One must remark and admire the experimental technique which, although sometimes open to criticism, reveals nevertheless the ingenuity and cleverness associated with Zondek's name. A bibliography of 269 titles and a summary of the work on the subject prior to 1935 are included.



BIOMETRY

STATISTICAL ACTIVITIES OF THE AMERICAN NATIONS. 1940. *A compendium of the statistical services and activities in 22 nations of the Western Hemisphere, together with information concerning statistical personnel in these Nations.*

Edited by Elizabeth Phelps. *Inter American Statistical Institute, Washington, D. C.* \$2.00. 9½ x 6; xxxi + 842; 1941.

This volume, prepared under the direction of the Temporary Organizing Committee of the Inter American Statistical Institute, has for its aim "to present a current account of the statistical services and activities of the American nations, together with a partial biographical list of the principal statistical personnel in those nations other than the United States." It is the outgrowth of the realization for some years past of the need to bring

into closer relation the statisticians of the various American countries and to make them acquainted with the fact-gathering activities of these different countries and the publications that are the outgrowth of such activities. Each one of the 22 American republics is represented in a series of descriptive papers. These are summarized both in the language of the country and in English. The articles cover such topics as the system of official statistics, including a discussion of censuses and a list of the principal government agencies which compile statistics; principal official serial statistical publications; statistical educational facilities; statistical library facilities; statistical societies or associations; and principal non-official or semi-official statistical agencies and their serial publications. One of the important features of the volume is the Biographical Directory of Statistical Personnel which covers 58 pages. Three appendixes contain general information on Statistical sources, Notes on the statistical section of the Eighth American Scientific Congress, and the Inter American Statistical Institute. An excellent index completes the volume.

STATISTICAL ATLAS OF SOUTHERN COUNTIES. *Listing and Analysis of Socio-Economic Indices of 1104 Southern Counties.*

By Charles S. Johnson and Associates: Lewis W. Jones, Buford H. Junker, Eli S. Marks and Preston Valien; Consultants: Edwin R. Embree and W. Lloyd Warner. *University of North Carolina Press, Chapel Hill.* \$4.00. 10 x 7; x + 355; 1941.

The sociological features of thirteen Southern states, by counties, are analyzed in this atlas. A great number of these features concern the educational characteristics of the areas, showing by race the expenditures per student percentage attendance, type and value of the schools, and per cent of illiteracy. The remaining features concern economic characteristics, including types of occupations, ownership and tenancy, order of major crops, and per capita wealth. From an analysis of these characteristics the counties have been classified into cultural types. It was found that geographical propinquity does not necessarily result in similar county types. This and other observations are briefly discussed, most of which have long been known but have not been adequately expressed quantitatively. Though doubtful, it is to be hoped that the toil and expense of preparing this volume will be warranted. The information might prove of value to leaders in rural educational programs because of the close interrelationship between the school and the socio-economic conditions of the surrounding area. The bibliography contains approximately 600 references.

THE SECOND YEARBOOK OF RESEARCH AND STATISTICAL METHODOLOGY. *Books and Reviews.*

Edited by Oscar Krisen Buros. The Gryphon Press, Highland Park, New Jersey. \$5.00: Less ten per cent on orders sent directly to The Gryphon Press. 10½ x 7½; xx + 381; 1941.

The second volume of this compilation is considerably enlarged. It contains reviews of 359 books published in English since 1933, of which 125 appeared in the first volume (noted in Q. R. B., Vol. 14, p. 378). The reviews have been culled from 283 journals. Unquestionably a useful source of information, this yearbook is also entertaining, and sometimes embarrassing for book reviewers. The editor would like to make the *Yearbook* an annual publication if funds could be obtained; otherwise it will remain biennial. Other and more ambitious changes are contemplated, including the review of articles as well as of books. The value of this proposal is doubtful.



THE BULLETIN OF MATHEMATICAL BIOPHYSICS. *Volume 4, Number 1, March, 1942.*

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: Diffusion as a Function of Aggregates in Colloidal Media, by Herman Branson; A Theory of Steady-State Activity in Nerve-Fiber Networks: IV. N Circuits with a Common Synapse, by Alston S. Householder; A Kinetic Theory of Diffusion Forces in Metabolizing Systems, by H. D. Landahl; Suggestions for a Mathematical Biophysics of Auditory Perception with Special Reference to the Theory of Aesthetic Ratings of Combinations of Musical Tones, by N. Rashevsky; Non-Linear Excitation Theory: Non-Accommodative, Sub-Threshold Effects, by Alvin M. Weinberg.



PSYCHOLOGY AND BEHAVIOR

TERRITORIAL AND MATING BEHAVIOR OF THE HOUSE WREN. *Illinois Biological Monographs, Volume XVIII, Number 3.*

By S. Charles Kendeigh. The University of Illinois Press, Urbana. \$1.50. 10½ x 7; 120; 1941 (paper). This exhaustive and valuable study of the house wren is the result of 19 years of observation of 142 male and 147 female wrens on a 15-acre estate. The results make it obvious that an intensive directive study reveals many facts otherwise not ascertained in casual field observation.

Adult males that have previously nested almost invariably return to the same territory that they formerly occupied, or they establish a new territory adjacent to it. The return of adult females to their former nesting

areas is almost as regular. The female does not defend territory or recognize the limits of territory as established by the male. When the female appears confined to a territory, it is due to her nest-box being centrally located within the territory, to her being chased out of neighboring territories, or to the male's adjustment of the outlines of his territory to coincide with her movements.

Territorial boundaries are frequently in a state of flux and rarely remain uniform throughout the season. These changes are caused by early arriving males attempting to take possession of very large territories, parts of which they are forced later to yield, to the impact of new males arriving and carving out territories, to variations in the activity and feeding areas of the female mate, to the shifting population of both males and females between the first and second breeding periods, and the necessity for remating. Territory is maintained throughout each breeding period and breeding season, although there may be some decrease in activity as nesting progresses. The non-breeding population of males varies from 28 to 35 per cent of the total male population and in the females from 13 to 20 per cent of the total female population. Except for the fact that only the male sings, sex recognition is based on differences in behavior of the two sexes. Later, there may be recognition of each other as individuals through characteristic mannerisms. Remating of a pair the following year occurred in 42 per cent of the cases where both birds of the pair survived and returned to the locality.

Besides the conclusions derived from the writer's observations, case histories of territories of individual males compiled during the course of this work are given "in order to make available to others the vast amount of information that accumulated at the Baldwin Bird Research Laboratory from 1914 to 1939."



DEVELOPMENTAL DIAGNOSIS: *Normal and Abnormal Child Development. Clinical Methods and Practical Applications.*

By Arnold Gesell and Catherine S. Amatruda. Paul B. Hoeber, Inc., New York. \$6.50. 9½ x 6½; xiii + 447; 1941.

A series of publications on the pioneer work of Gesell and his co-workers has preceded this book. *Developmental Diagnosis*, which is destined to become a classic, has the advantage over these earlier books in that it is much more inclusive as regards subject matter. It also gives the most concise and workable presentation to date of the Gesell clinical testing material. In the preface Gesell states that:

Observations of normal behavior threw light on maldevelopment; and the deviations of development in turn helped to expose what lay beneath a deceptive layer

of "obviousness" in normal infancy. We have come to sense the identity of the developmental processes which in equal measure determine the reaction patterns of the intact and the defective child, the well endowed, the partially endowed, and those blemished by injury and disease.

It is these deep, determining developmental processes which must inevitably come within the scope of clinical medicine. In preparing this volume we have had much in mind the medical student who in private or public capacity will soon be confronted with varied and exacting problems which concern the developmental welfare both of normal and abnormal children.

From a study of the genesis and growth of patterns of behavior Gesell has been able to formulate concrete norms of maturity which have been given thorough practical tests and have proved dependable "not only in the study of normal variations of development, but in the diagnosis and supervision of pediatric, neurological and psychiatric conditions."

The emphasis throughout the book is on diagnosis. In the first section the basic principles and methods are first outlined and the nature of behavior and of mental growth discussed. Chapter III, by far the longest in the book, is the most basic in that it "integrates the developmental tests, the behavior characteristics, and the growth trends of the behavior patterns for the period from 4 weeks to 3 years. This chapter is organized for convenient reference and is illustrated with over a hundred photo-tracings of normative behavior patterns." Part II, dealing with defects and deviations of development, discusses problems of differential diagnosis, amentia and retardation, amentia of high grade, low grade amentia, endocrine disorders, convulsive disorders, the neurological diagnosis of infant behavior, cerebral injury, special sensory handicaps, prematurity, precocity, environmental retardation, and clinical aspects of child adoption. Part III is concerned with the protection of early child development—diagnosis and guidance and development supervision. Four appendices give details concerning technique, charts, equipment, and cinematic case studies. The volume is provided with an excellent working index.



BASIC PROBLEMS OF BEHAVIOR.

By Mandel Sherman. Longmans, Green and Company, New York, London and Toronto. \$3.00. 8½ x 5½; vi + 440; 1941.

Many books concerned with personality and adjustment suffer from an excess of clinical evidence and a lack of scientific fact. This book, an elaboration of the author's *Mental Hygiene and Education* (1934), demonstrates that, in the investigation of problems of behavior, clinical and experimental evidence can be brought together with successful results. This alliance is accomplished by the selection of suitable experiments from the huge amount of psychological literature, and practical illus-

trations furnished from clinical data. The opening pages present a systematic discussion of emotion as a foundation for the following chapters on motivation and frustration (including experimental neurosis), personality, adjustment mechanisms, attitudes, conflicts, neurosis, and mental abnormalities. A valuable chapter on delinquent behavior discusses current theories of the psychogenic basis, personality, and treatment of this problem. Gathering together as much data as it does, this book should prove valuable for reference as well as for use as a text, and may well encourage a closer association between psychologist and psychiatrist, as the author suggests. One might wish a more critical treatment of personality tests and procedures used in measuring attitudes. A 16-page bibliography and index are included.



BREATHING CAPACITY AND GRIP STRENGTH OF PRESCHOOL CHILDREN. *University of Iowa Studies in Child Welfare, Volume XVIII, Number 2.*

By Eleanor Metheny. University of Iowa Press, Iowa City, Iowa. \$1.35 (paper): \$1.70 (cloth). 9½ x 6½; 207; 1940.

This investigation is designed to study the possible relationship of breathing capacity and grip strength to health and physical condition. Until now data concerning this problem in preschool children have been scarce. Special spirometers and dynamometers were constructed suitable to the physical requirements and need for special motivation of the children. Complete information was obtained concerning anthropometric measurements, intelligence scores, health and fatigue ratings, sex, and age. In the analysis of data on approximately 200 children the intelligence quotient was found to be unrelated to either grip strength or breathing capacity but height was most highly correlated with both factors. It is doubtful that breathing capacity is related to health of preschool children, but on the average the children with higher physical condition ratings had greater grip strength. The material suggests that the latter variable may be related to the run-down condition preceding a cold. This careful study justifies further investigation of grip strength as a functional test for children.



A BEHAVIOR STUDY OF THE COMMON TERN (*STERNA HIRUNDO HIRUNDO* L.). *Proceedings of the Boston Society of Natural History, Vol. 42, No. 1.*

By Ralph S. Palmer. Society of Natural History, Boston, Mass. \$1.00. 9 x 6; 119 + 14 plates; 1941 (paper).

A number of notable field studies and reports on the natural history of the common tern have appeared in recent literature, but none has dealt so fully with the

individual and social behavior of the bird as the present investigation. The author's careful field observations extending over several years in the terneries at the Sugarloaf Islands off Sagadahoc County, Maine, are herein set forth with an excellent measure of scientific exactness and clarity. The detailed behavior of the tern from the time of its arrival at the ternery, through the mating, brooding, and rearing seasons, makes up the greater portion of the report. Notes on the requirements for a successful tern colony (isolation, food, and cover), the economic importance of the bird, as well as a list of its predators are included. The report concludes with an extensive bibliography, several charts, and a number of plates depicting the habitual activities of the tern.



SCHIZOPHRENIA IN CHILDHOOD.

By Charles Bradley. *The Macmillan Company, New York.* \$2.50. 8 x 5½; vii + 152; 1941.

As indicated by the title, the subject matter of this book is concerned with the schizophrenic reaction as it is seen in children. In the first three chapters the author gives a brief but appropriate summary of the development of the present-day schizophrenic concept through the influences of Kraepelin, Bleuler and Meyer. The viewpoint from which the remainder of the book is written seems to emphasize the "disease entity" rather than the "reaction type" concept, and the value of the book as a contribution to the literature is correspondingly weakened. Indicative of the contents and organization of the material are the chapter headings: Incidence, Symptomatology, Course, Types, Etiology, Psychopathology, Laboratory Findings, Anatomical Pathology, Diagnosis. The author leans to a constitutional basis, with secondary, precipitating situation factors as causative agents. The treatment is descriptive rather than dynamic. There is a bibliography of 118 titles. Subject and author indices are included.



A NEW TEST FOR THE DETECTION OF COLORBLINDNESS.

By P. B. Willberger. *College Book Company, Columbus, Ohio.* \$3.00. 9 x 6; 22; 1941.

Many people who are classified as colorblind by the usual tests are not truly colorblind but have varying degrees of weakness in color perception. The writer of this book objects to the use of such tests for this and other reasons. He recommends the use of color "chips," or rectangles, on which the subject fixes for a short period of time. Upon shifting the fixation point the normal person (or a person who is only color weak) sees the complimentary color after-image, whereas the totally colorblind person sees a white rectangle.

The book contains a brief description of the physiology of color perception, directions for administration

of the test, and several pages of color "chips." For some purposes this method may be useful, but in general people who administer tests of color perception are interested in detecting color weak individuals as well as those who are totally colorblind.



SOCIAL CASE RECORDS FROM PSYCHIATRIC CLINICS with Discussion Notes.

By Charlotte Towle. *The University of Chicago Press, Chicago.* \$3.00. 9 x 5½; xii + 455; 1941.

This book has been written primarily for use in the author's classes in psychiatric social work at the University of Chicago. The organization of the material is, accordingly, for usefulness in study and discussion. In a nine-page introduction the author formulates in concise and lucid form the general conceptual background against which the present-day psychiatric social worker operates. The remainder of the book is devoted to a presentation, in detail, of psychiatric social worker contacts with nine separate cases. The presentation of each case is followed by discussion notes and a pertinent list of references. There is an index. This book is recommended as an authoritative and practical contribution to its field.



*CHILD PSYCHOLOGY: *Child Development and Modern Education.*

Edited by Charles E. Skinner and Philip L. Harriman. With the Collaboration of Amy F. Arey, L. A. Averill, Lorin E. Bixler, E. A. Bond, J. W. Charles, and Others. *The Macmillan Company, New York.* \$3.00. 8½ x 5½; xii + 522; 1941.

A symposium of the general subject of child psychology. Fourteen different contributors are included. The general plan is a presentation of the problems of child psychology and a description of the methods employed in the scientific study of children. Throughout, the normal child is regarded as an integrated, growing personality. The book is well set-up and organized and the material is lucidly presented. Lists of references follow each chapter. In an appendix a brief, comprehensive outline of each chapter of the book is given. There are subject and author indices.



MENTAL HYGIENE IN EDUCATION.

By Ernest W. Tiegs and Barney Katz. *Ronald Press Company, New York.* \$2.75. 8 x 5½; xiv + 418; 1941.

A mental hygiene book for teachers, administrators, supervisors and students of psychology. The material is presented in three parts: Part I. The nature and

origin of personality difficulties; Part II. Improving personal and social adjustment; and Part III. The more serious personality difficulties. The scope of the material is broad and the aim of the authors commendable, but the treatment inevitably reflects the doctor of philosophy rather than the doctor of medicine, and is academically descriptive rather than dynamic. It is doubtful whether the book will prove a practical guide in handling the personality problems of school children. A list of references follows each chapter and there are author and subject indices.



VISION. *A Study of its Basis.*

By S. Howard Bartley. *With an Historical Perspective* by Edwin G. Boring. D. Van Nostrand Company, New York. \$3.50. 8½ x 5½; xv + 350; 1941.

A handbook on the psychophysiology of vision. The author presents material selected from the psychology of vision for which present day neuro-physiology has something to offer, and discusses certain related visio-sensory phenomena for which physiology must provide an answer. Aspects of vision touched on are indicated by some of the chapter headings: Forms of brightness discrimination, Entoptic stray light, Repeated stimulation, Flicker, Perception of movement, Neural interaction, Contour, The electroretinogram, The optic-nerve discharge, The cortical response. References are appended to each chapter, and there are name and subject indices.



JUVENILE DELINQUENCY: *A Comparative Study of the Position in Liverpool and England and Wales.*

By J. H. Bagot. Jonathan Cape, London. 5s. 8½ x 5½; 93, 1941.

This book presents the first of a new series of studies of social problems issued from the Division of Statistics in the Social Science Department of the University of Liverpool. The study is designed to throw light on the question of why the trend of juvenile delinquency is beginning to soar again with the advent of the present war. The study consists of a comparison of the position in Liverpool, England and Wales, and is based on detailed analysis of records of juvenile delinquency. The conclusions and recommendations are summarized in one of the final chapters.



ANXIETY AND ITS TREATMENT *with Special Reference to Alcoholism.*

By John Yerbury Dent. John Murray, London. 3s. 6d. 7½ x 4½; 124; 1941.

This is a consideration of the problem of alcoholism viewed as a symptom of an underlying anxiety. How-

ever, the author writes from the viewpoint which is of doubtful helpfulness and accuracy, that anxiety is essentially a chemical and physical manifestation rather than a manifestation of personality malfunction. Alcoholism is regarded as a chemical disease. One chapter is devoted to vitamin B deficiency. In another the treatment of addiction by apomorphine is described.



PARS PRO TOTO. *Ein Beitrag zur Pathologie Menschlicher Affekte und Organfunktionen. Schriftenreihe zur Deutschen Medizinischen Wochenschrift, Herausgegeben von R. Siebeck und V. v. Weizsäcker, Heft 5.*

By Rudolf Bilz. Georg Thieme Verlag, Leipzig. RM. 9.75 (outside of Germany). 8½ x 5½; 318; 1940 (paper).

The author offers in this treatise a biologically oriented contribution to the pathology of human emotions and organic functions (neuroses). The investigation will interest all students of the "mind-body" problem, particularly biologists, psychologists, and psychiatrists.



**DE OMNIBUS REBUS
ET QUIBUSDEM ALIIS**

NATURAL HISTORY AND THE AMERICAN MIND.

By William Martin Smallwood in Collaboration with Mabel Sarah Coon Smallwood. Columbia University Press, New York. \$4.25. 9 x 6; xiii + 445; 1941.

This is a pioneering work. Within the past few years a number of biographical works dealing with the naturalists of America have appeared, but this is the first one to focus its emphasis exclusively on the effect of their lives and work on contemporary and subsequent thought. The men and women whom the authors have selected for special attention are not by any means the greatest, but those whom they consider to be the most significant: those who occupy not the mountain passes but the cross roads on paths to knowledge. Therefore, the personnel discussed in a work of this sort is largely a matter of opinion, and the present reviewer feels that the omission of Robert Chambers, whose *Vestiges of Creation* prepared the way for Darwin is very definitely a defect. Certainly Chambers through his influence on Darwin has affected later scientific thought as much as, if not more than, that other pre-Darwinian evolutionist, Rafinesque, whose erratic figure appears and reappears throughout the pages of this book. And the treatment of Amos Eaton seems somewhat out of proportion when compared to, for instance, that accorded Agassiz.

Except for such instances, however, the selection of personnel is above criticism. There is practically no naturalist who lived in the United States prior to 1850 who is not mentioned in the pages of this work. Some-

times the notice seems inadequate. For example, Charles Alexandré Lesueur is mentioned because he made the drawings for Godman's *Natural History*, thus setting a new standard for scientific illustration. Nothing is said about his romantic career with the ill-fated expedition of La Perouse, of which he was the only member to escape the destruction which overtook it. Neither is anything said about Lesueur's systematic work on pelagic mollusca, and only the briefest possible mention is made of his part in the establishment of the intellectual capital of the United States at New Harmony.

Again, John Bartram receives a great deal of attention, which of course he merits, but nothing is said about his spectacular discovery of *Franklinia*. But of course, if the authors had attempted to please all their potential readers (whose name should be Legion) they would have produced a work the size of the Cambridge Natural History. The chapter dealing with the sixteenth and seventeenth century writers was an eye opener to this reviewer, as was also the story of Jane Cloden of the eighteenth century, who was the first woman to take up any kind of scientific activity.

Perhaps the most original, and hence the most important chapter, is that dealing with the manufacturers of scientific instruments. We all use microscopes, but what do we know about Spencer, Tolles, Gronow, and Zentmayer? How many who use Spencer instruments know that at the age of sixty Spencer lost his entire plant, stock, and records in a fire, and then proceeded to set the entire world an example of courage and heroism by starting over again from scratch, five years later winning a gold medal at the Paris exposition?

To the authors of this work America means only the Atlantic seaboard of the United States. This example of inverse synecdoche leads them to repeat the popular error that the Museum of the Library Association in Charleston, South Carolina, was the first to be established in America. As a matter of fact, the Natural History Museum established by Kino at Matapé, Sonora, antedated that at Charleston by more than a century. Also, the authors' contention that American culture originated on the Atlantic seaboard can hardly be maintained, for when Harvard was founded in 1638 there were at least four universities on the Pacific slopes of Latin America, one of which at Leon, Nicaragua, had been in operation since 1523.

A more adequate index and a chronological table would have added to the efficiency of the work, as would have better documentation. But despite these criticisms the book is truly monumental and deserves universal circulation.



THE ROAD OF A NATURALIST.

By Donald Culross Peattie. Houghton Mifflin Company, Boston. \$3.00. 9 x 5½; ix + 315; 1941.

Not since the publication of *The Desert* and *The Mountains* has the present reviewer come across a more beautifully expressed appreciation of nature than this work by Peattie. Like Van Dyke, Peattie understands the truth of the statement of a late philosopher, that "There is more real beauty in what science has to tell us of the chemistry of a distant star, or of the life history of a protozoon, than in any cosmogony produced by the creative imagination of a pre-scientific age." Both Van Dyke and Peattie give free rein to creative imagination, but both confine their statements to what science can reveal to us about the natural countryside. Here the resemblance ceases. Van Dyke is an art critic, Peattie is an artist. Instead of the impersonal and objective attitude of Van Dyke, Peattie is personal and subjective, and identifies himself with the desert and the mountains that he loves. In his case the antithesis between man and nature does not exist. Like the child in one of Kipling's *Just So* stories, he fades away into the landscape, and becomes part of nature. The mantle that has fallen upon his shoulders is not that of Van Dyke, but that of William Bartram, that gentle soul of an earlier century, who was so distressed by the cumber and entanglement of a war torn world that he retired to the wilderness to commune with nature and nature's God.

Peattie is not inspired by the desert so much as by the feelings which it evokes within him. His poetic descriptions alternate with meditations of an intimate nature upon the deeper things of life, which will be found comforting by those who have endured the same sorrows, and there are many such, but they are not articulate and we seldom hear about them. The world has great need today of the mystic vision. It must be a great satisfaction to the author to know that he is helping to meet this need.



RESEARCH—A NATIONAL RESOURCE. II.—*Industrial Research*. December, 1940. Report of the National Research Council to the National Resources Planning Board.

National Research Council. Government Printing Office, Washington. \$1.00. 11½ x 9; xi + 370; 1941 (paper).

Under the direction of the National Resources Planning Board three surveys have been made concerning research as a national resource, not only in relation to the present defense effort but also to developments in the post-defense period. The first of these reports, on "Relation to Federal Government of Research," has been published. The third, "Business Research," is in preparation. The second, the present volume, has been prepared by 26 outstanding leaders in research. From a summary of the findings we note the following:

Continuous and increasing application of science by industry is contributing most significantly to the high

standard of American living. Viewed in this light industrial research is a major national resource. . . . American industry employs over 70,000 research workers in over 2,200 laboratories at an estimated annual cost, based on an average of figures reported, of the order of \$300,000,000. . . . Industrial research is possible for all industrial units, small and large. . . . Industry looks to the universities for trained technical men, and for principal advances on the frontiers of science. . . . There is opportunity for some American university to establish a comprehensive curriculum in applied mathematics. The number of men engaged in applied mathematics is comparatively small but their work is extremely significant.

Recommendations, in summary form, are also made to industry, to labor and industry, and to the Government for the further extension of research in industrial fields.



* SCIENCE versus MATERIALISM.

By Reginald O. Kapp. *Methuen and Company, London.* 10s. 6d. $7\frac{1}{2}$ x $5\frac{1}{2}$; 280; 1940.

The author of this book is an engineer who seems, unfortunately, unfamiliar with the concept of *integration* in human biology. He attempts to answer, to his own satisfaction, the question "Is matter the only reality?" His revival of the battle between science and religion and materialism and vitalism would seem to be an earnest battle against windmills. The book is divided into three parts: I. Clearing the ground; II. Double determinateness; and III. The material universe.

By circuitous routes he clears his mind by resorting to the dichotomy of living and lifeless substance (i.e. organic vs. inorganic) and asserting that living substance is subject to a double set of restrictions, that its behavior is *more* determinate than that of lifeless substance. This "double determinateness" is regarded as evidence for vitalism. Likewise, living substance is constructed to a "specification," i.e. is not merely the result of shaking down, as in crystal formation and other inorganic aggregates. Many references are made to the views of various biologists, philosophers, and physicists, both ancient and modern.

It is felt that the puzzled reader will find little help in this exposition, and the casual reader little interest.



PHOTOGRAPHIC EMULSION TECHNIQUE.

By T. Thorne Baker. *American Photographic Publishing Company, Boston.* \$4.00. $7\frac{1}{2}$ x $5\frac{1}{2}$; xii + 263; 1941.

"This book is intended not only to be a guide to practical emulsion making, but as a textbook for technical students, industrial chemists, and photographers generally, who are anxious for their own reasons to prepare emulsions of various types and speeds." Although the

range of commercially produced sensitized paper, glass, and film is wide, the photographer occasionally requires an emulsion outside of this range and in such a small quantity as to make commercial production impossible. The writer thoroughly explains the technique of preparing emulsions, including selection of materials, laboratory layouts, coating, color, x-ray, ultraviolet, grain, speed, etc.

For deeply involved amateur photographers, study and experimentation with emulsions provides a fascinating hobby full of possibilities. For them this book may be recommended as an excellent guide. Yet a simple reading of these pages cannot but broaden the knowledge of those who depend entirely upon commercial products. Included are many references and a complete index.



SOIL AND SENSE.

By Michael Graham. Preface by Sir E. John Russell. *Faber and Faber, London.* 7s. 6d. $7\frac{1}{2}$ x $4\frac{1}{2}$; 274; 1941.

The fertility of the soil is to agriculture what petrol is to a motor car—it is what keeps it a going concern. In this simply written and very understandable volume, Graham has brought out the fact that increased mechanization, with its counterpart, decreased animal populations, has resulted in a serious strain on the fertility of the soil. This condition is further aggravated by the excessive and unwise use of cheap chemical fertilizers. In non-technical language, the author discusses the natural fertility cycle of the soil, as well as crop rotation, and the importance of grasses and legumes in maintaining soil fertility, and encourages the farmer to avail himself of the scientific tests now available to determine the needs of his soil, and to make up for the depletions with a good grade of chemical fertilizer. There is also a strong plea for landlords to assist tenants in supplying the needed fertilizer.

Since the book is about British agricultural problems there is little beyond the very broadest considerations which will be of value to the American farmer. A short list of references and an index are appended.



THE ROCKEFELLER FOUNDATION: *Annual Report for 1940.*

By Raymond Fosdick. *The Rockefeller Foundation, New York.* Free. $8\frac{1}{2}$ x $5\frac{1}{2}$; xv + 473; 1941 (paper). In the first part of this report is given President Raymond B. Fosdick's review of the year's work of the Foundation. Then follow detailed reports for the different divisions: International Health, Medical, Natural and Social Sciences, Humanities, and Work in China. Appropriations for the year amounted to

\$9,854,497. Of this sum, 77 per cent was for work in the United States and 23 per cent for work abroad. Public health received the largest share, followed by the natural, social and medical sciences, humanities, and rural reconstruction in China, in the order named. The war curtailed the work in some of the European countries but appropriations went to 44 countries in Europe, Asia, Africa, and the Americas. The activities of the Foundation, extending into all fields of intellectual endeavor, represent wise and careful planning on the part of those who have the responsibility of disbursing the funds. The largest single appropriation went to the University of California for the construction and housing of a giant cyclotron.



BY LIGHT OF SUN.

By *Elsie Symington*. With Foreword by *Richardson Wright*: Woodcuts by *Claire Leighton*. G. P. Putnam's Sons, New York. \$2.00. 8 x 5½; x + 196; 1941.

Mrs. Symington's autobiography is the story of a sensitive woman's successful search for a way of living which would provide the widest scope for her physical and mental energies. Because the environment she sought turned out to be a special sort of house in a special sort of garden, the casual reader may be inclined to dismiss the work as just another garden book. It is a great deal more than that, for its author is a peculiarly articulate person, able to analyze and explain with great skill the various "drives" which warred within her and to make it understandable just why she finally chose to use all her force in the creation of a vast garden in which things are permitted to grow under the circumstances in which they grow best. In not many autobiographies is the author more precisely aware of her place in the scheme of things, her capacities and limitations. Women seem to have a talent for self-revelation and Mrs. Symington has cultivated her large share of that talent to make a book which has something in common with the great self-portraits of the past.



BIOLOGICAL STAINS: A Handbook on the Nature and Uses of the Dyes Employed in the Biological Laboratory. Fourth Edition Revised.

By *H. J. Conn*. With the collaboration of *J. A. Ambler, R. W. French, W. C. Holmes, et al.* Revised with the assistance of *J. T. Scarnan, Anis P. Bradshaw, and Mary A. Darrow*. Biotech Publications, Geneva, N. Y. \$3.40. 8 x 5½; 308; 1940.

This recognized and authoritative handbook of dyes employed in the biological laboratory has been given a very careful revision and brought completely up-to-date. New material embodied includes description

of thirteen dyes not previously considered. The subject covered so adequately by this book is becoming a field for more and more precise knowledge all the time and hence the urgent need for just such a volume as this. In addition to the succinct presentation of the nature and uses of the various dyes themselves, the book includes a discussion of the history and theory of staining, and the spectrophotometric analysis of dyes. The appendix contains much valuable information arranged in convenient tabular form. The volume is concluded with a complete bibliography and index. To students, technicians, and seasoned investigators everywhere, this manual of stain technology—one of the few acceptable to the discriminating scientist—should prove of inestimable and increasing value, as its previous editions have done.



AMERICA'S HOUSEKEEPING BOOK.

Compiled by *New York Herald Tribune Home Institute*. Charles Scribner's Sons, New York. \$2.00. 8½ x 5½; xxiv + 607; 1941.

A manual for the housewife. The book has been in the making for upwards of 15 years. It developed out of numerous letters and telephone calls from housewives for aid on household matters. Frequently, long and difficult research was necessary by the Institute staff to find solutions to some of these problems. The material is well organized under three headings: Home organization; Housekeeping methods; and Operation and maintenance of the home. The index, which covers 28 closely printed pages, gives some indication of the number of subjects covered. We mention only a few of these: electric shock, medicines, removing stains, heating systems, household pests, electrical repairs, paints and stains, repairing furniture, doors, etc., treatment of walls, and soaps. Many illustrations are included.



DIRECTORY OF MICROFILM SOURCES including Photostat Service.

Compiled by *Rose C. Cibella*. Special Libraries Association, New York. 75 cents. 10 x 7; vii + 56; 1941 (paper).

A directory for librarians, research workers, and industrialists. It has been issued to make available the data now in hand, but a revised edition is contemplated which will furnish a much more complete set of records. There are listed 202 universities and libraries which now provide microfilm or photostatic service, also a number of commercial firms. A group of sample order forms in use by various institutions, a geographical index of microfilm sources and an index to equipment help to make this directory extremely useful to those wishing to avail themselves of the fine opportunity offered by libraries in the United States, Canada, and England.

THE QUARTERLY REVIEW *of* BIOLOGY



THE RELATION OF ADAPTABILITY TO ADAPTATION

By G. F. GAUSE

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THIS article is the first in a series of essays on the ecological aspects of some problems of the origin of species. Its chief purpose is to summarize the results of my recent experimental investigations on the relation of adaptability to adaptation in unicellular organisms, which were published in the Russian language in various biological journals of U.S.S.R., and to coördinate the results thus gained with the rest of our knowledge in that direction.

The study of the mechanism of the adaptive process is essentially an ecological problem. When a population of a given species is subject to the action of altered environmental conditions, for example, the increased concentration of salts or of some other chemical substances in the medium of an aquatic animal, a number of complicated processes sets into operation. On the one hand, there exist inherent initial differences in susceptibility to the new conditions among members of a given population of individuals. Further, there exist inherent differences in adaptability of different individuals to the altered environmental situation. Adaptability is here used as the capacity for adaptive modification in individual development, which is due to a number of physiological mechanisms acquired in the previous history of a given species.

What will be the effect of natural selection under all these circumstances? Will it favor an outstanding initial strength, or an extremely rapid adaptability, or both of these? What will be the results of selection in the populations of the various

species and under different factors of the environment?

It will be useful to consider separately two different possible situations: First, the mechanism of the adaptive process to the environment which is gradually changing. It is this problem of changing environment which is only considered in the present article. Experimental work along this line has led to the discovery of the peculiar relation of adaptability to adaptation within the population of one and the same species. It has also shown the importance of the magnitude of genetic diversity in adaptability of different individuals in a population, as compared to the magnitude of diversity of the same individuals in their inherent initial strength.

Second, it will be appropriate to treat the case when some environmental factor has changed from one to another of relatively fixed values. How will natural selection work to stabilize the population under the new steady circumstances? The consideration of this problem is reserved for subsequent publication.

THE IMPORTANCE OF ADAPTIVE MODIFICATIONS FOR EVOLUTION

The part played by adaptive modification in evolution has been much less than adequately valued in the recent development of biological thought. As Pearl (1939) truly remarked, this is an obvious consequence of the trend given to biological philosophy by Weismann and Bateson, with their emphasis upon the entailed or endowed element in the whole biological picture.

It is well known that all organisms have the capability to alter themselves to meet the fleeting changes in their circumstances. Various adaptive modifications acquired under the effect of environment are not hereditary, but the very feature of adaptability is undoubtedly an outcome of the long historic process of natural selection. Adaptability is useful, and natural selection has provided for that specific architecture of physiological processes that guarantees the production of appropriate modifications. Whether or not all modifications are actually adaptive is a problem in itself, and this subject will be given due consideration in one of the subsequent articles.

Since adaptive modifications are not hereditary, they are usually believed to be of no importance for evolution processes. However, there are also advocates of a different attitude. The reasoning of Lukin (1936) is as follows. Adaptations of organisms to environment are of two kinds: First, non-hereditary alterations under the effect of environment upon physiological systems of the developing organism. For example, animals grown in low temperatures are larger. This is useful for temperature regulation in a cold climate, because of the decrease of surface per unit of body volume. Second, a similar gain in body size can be brought about by chance mutation, without any action of low temperature.

This parallelism of hereditary and non-hereditary variations is rather widely spread and it can be satisfactorily explained by developmental physiology. In both cases the alteration of an organism is usually due to a change in the relation between rates of some biochemical reactions. Whether this relation is shifted because of the altered temperature conditions, or because of variation in quantity or quality of catalyzers, in its turn depending on mutation in the hereditary material, the effect of both these different causes is the same. Sometimes it is stated that non-hereditary modifications duplicate hereditary ones. The former are then called "phenocopies" (Goldschmidt, 1938). Sometimes the terminology is reversed and mutations are called "genocopies" of non-hereditary modifications (Schmalhausen, 1938).

Are there some reasons to suspect genocopies to be in some respects particularly useful in the mechanism of the adaptive process? Lukin (1936) recently pointed out that there are at least two reasons for such a belief. On the one hand, a

casual genocopy can be suspected to be summed up with the useful phenotypic modification, and consequently produces a particularly vigorous organism in some specific respect. This is the principle of intensification of characters. On the other hand, some useful feature of organization by the way of genocopy is developed relatively independently of the accidental interplay of environmental factors at the time of ontogenesis, and in this respect it might be advantageous over the common adaptive modification. This is the principle of autonomization of characters. In other terms, according to this conception, natural selection will favor distribution in populations of genocopies augmenting and improving the external expression of adaptive modifications. If after such a selection a population returns to the original conditions of its existence, the former adaptive modifications appear to become hereditary. This is one of the central points of the whole theory, which should consequently be called a hypothesis of hereditary fixation of adaptive modifications by means of natural selection of genocopies. In the light of this conception adaptive modifications prepare the way for the subsequent evolutionary advance.

THE MAGNITUDE OF ADAPTIVE CHARACTER

The theory outlined above evidently operates with the concept of magnitude of adaptive characters. This magnitude means the value of those features or characters which are useful, and which determine the survival of an individual in the process of natural selection. It is admitted that the greater is the magnitude of some adaptations, the more are the advantages associated with the possession of them.

Let us take for example the case of adaptation of an aquatic animal to the increased salinity of the medium. It will be seen that a part of total adaptation, i.e. of total resistance to salinity observed under the new environmental conditions, will form a feature of organization deeply rooted in the previous history of a given species. We mean the original resistance to salinity in the initial conditions, which would be maintained if the environmental conditions remained unaltered. It is this initial inherent adaptation which can be augmented or weakened by means of genocopies.

The other part of total adaptation observed under new environmental conditions represents adaptive modification. It is the outcome of onto-

genic adaptability, the adaptive response of the organism to the altered conditions of its existence. This second part of total adaptation is in its turn subject to hereditary alterations.

Summarizing, it can be stated that the total magnitude of adaptation in the case of some adaptive characters (but certainly not in all of them) can consist of two components: initial adaptation and acquired adaptation. Hence:

$$\left\{ \begin{array}{l} \text{The magnitude} \\ \text{of adaptive} \\ \text{character} \end{array} \right\} = \left\{ \begin{array}{l} \text{Initial adaptation before} \\ \text{the beginning of action} \\ \text{of a specific environmen-} \\ \text{tal change. Depends upon} \\ \text{previous history of a given} \\ \text{group of individuals} \end{array} \right\} + \left\{ \begin{array}{l} \text{Adaptive modifi-} \\ \text{cation acquired} \\ \text{under the action} \\ \text{of the specific} \\ \text{environmental} \\ \text{change} \end{array} \right\}$$

The theory outlined above can now be formulated thus. A casual increase of initial adaptation by means of genotypic alteration must be summed up with the magnitude of adaptive modification, and consequently yield a larger value of total adaptation useful for an organism. It is only with such summation of adaptations that natural selection could augment adaptive modifications by genocopies resembling them.

THE CONSTANCY OF TOTAL ADAPTATION IN SOME ADAPTIVE CHARACTERS

We have now sufficiently clarified some basic concepts underlying the theory of hereditary fixation of adaptive modifications by means of natural selection of genocopies, and we can now attempt to prove this theory by direct experiments. Is the genotypic increase of initial adaptation really summed up with the magnitude of adaptive modification?

This problem was analyzed for the case of adaptation of various species of the genus *Paramecium* to the increased salinity of the medium (Gause, 1939; Gause and Smaragdova, 1939; Smaragdova, 1940). Although paramecia are typical fresh-water inhabitants, some of them also dwell sometimes in saline environments (Quennerstedt, 1865; Florentin, 1899; Kahl, 1928) and even in marine water (Levander, 1894; Calkins, 1902; Smith, 1904). It is hence interesting to analyze

carefully the mechanism of their adaptation to the increased salinity of the medium.

Experimental adaptation of certain fresh-water ciliates to sea water was in recent years attempted by several authors. The delicate mechanism of the adaptive process, however, was not adequately analyzed. For example, Finley (1930) added sea water to mixed cultures of Protozoa and reported that in cases of direct dilution of cultures by sea water in increased proportions paramecia can tolerate up to 10–20 per cent, but in gradual adaptation, up to 100 per cent of sea water. These results were not confirmed by subsequent investigations. Yocom (1934), who also added sea water to mixed cultures of infusoria, observed the death of paramecia when the concentration of the added sea water attained 20–60 per cent. Frisch (1935, 1939) reported that paramecia cannot tolerate the concentration of sea water exceeding 40 per cent. Loefer (1939) also made some experiments in that direction.

In all these studies no attempt was made to evaluate the effect of natural selection in the experimental adaptation of paramecia to the increased salinity of the medium.

The first object of our investigations was to procure material with sufficient range of hereditary variations in respect to salt resistance. The isolation of single clones of infusoria from common wild cultures reveals usually only a narrow hereditary variability. Wild cultures are relatively homogeneous, because competition and natural selection are very keen in them, and only a few strong strains of paramecia usually survive. In this way relatively weaker clones drop out of the field of our observation.

In order to avoid this difficulty and to work with that wide range of hereditary variability which actually takes place in nature, and not only with a few clones which survive under some specific conditions, we isolated various clones at some stages following conjugation processes. According to older data of Jennings (1913), confirmed more recently by Raffel (1930), and also by Jennings, Raffel, Lynch, and Sonneborn (1932), recombinations of hereditary material at the time of conjugation produce numerous inherent variations in morphological and physiological characteristics of *Paramecium*.

The experiments were begun by induction of conjugation in a wild culture of *Paramecium aurelia* by a method described recently by Bar-

barin (1938). A dense suspension of paramecia about 3 c.c. of the volume was poured into a small, specially-constructed vessel, and for an hour bubbles of hydrogen were passed through it. Then the vessel was closed hermetically and the paramecia left for a night in the atmosphere of hydrogen at 25°C. Next morning air was bubbled through the liquid, and the paramecia were kept for a few hours in aerobic conditions. In consequence of such a procedure, numerous pairs of conjugants appeared in the wild culture of paramecia.

We isolated 28 conjugating pairs of *P. aurelia* into depression slides, which in their turn were put into large moist chambers kept at 20°C. On the following day both separated exconjugants (a and b) of each pair were again isolated into depression slides, and a day hence the products of the first division following conjugation (a_1 and a_2 from the first exconjugant, b_1 and b_2 from the second exconjugant) were isolated once more. In this way each pair of conjugants was the ancestor of the four separate lines of infusoria, a_1 , a_2 , b_1 , b_2 . Sonneborn (1937) has shown that the isolation of a clone in *Paramecium aurelia* at the stage of the first division following conjugation usually guarantees its hereditary homogeneity at later stages of vegetative reproduction.

We have isolated altogether $28 \times 4 = 112$ separate lines of *P. aurelia*. The four lines originating from the same pair of conjugants will be further called a family. It is known that owing to lethal combinations of hereditary material at the time of conjugation a number of lines subsequently dies out, and hence some of our clones soon disappeared. We have used in further work only 5 families of *P. aurelia*, in each of which survived all four lines. Consequently, the total number of lines of *P. aurelia* employed attained 20.

Paramecium aurelia was cultivated in Osterhout's saline medium of the following composition: NaCl—2.35 gr., $MgSO_4 \cdot 7H_2O$ —0.250 gr., KCl—0.050 gr., $CaCl_2$ —0.027 gr., water bidistilled in Jena glass—100 cc. This stock solution, in which the concentration of salts attained 2.7 per cent, was diluted before the experiments with bidistilled water 225 times by volume, so that the total concentration of salts attained finally 0.012 per cent. In the case of experiments with increased salinity, the stock solution was diluted with bidistilled water in such a way that the total concentration of salts attained 0.1, 0.5, 1.0 per cent,

etc. Paramecia were fed by suspension of *Bacillus subtilis* and of *Torula utilis* in the saline medium. The yeast *Torula* was previously cultivated in Petri-dishes on beer-wort agar medium, and with the aid of a platinum loop transported into the saline medium. We have isolated from hay infusion a strong strain of *Bacillus subtilis*, satisfactory by its nutritive properties for paramecia, which was further cultivated on a solid medium (5 per cent hay infusion plus 1.5 per cent agar-agar). The bacteria were also removed by a platinum loop from the solid medium and added to the suspension of yeast cells.

Two other species, *Paramecium caudatum* and *P. bursaria*, were cultivated in Beers medium of the following composition: $Ca(NO_3)_2$ —0.03 gr., KNO_3 —0.01 gr., $MgSO_4 \cdot 7H_2O$ —0.01 gr., H_2O —500 cm.³ The other details of cultivation were the same as with *P. aurelia*. For experiments with adaptation to salinity Osterhout's saline medium was used. This was added in various proportions to the Beers culture fluid. All these experiments were run at 25°C.

In further work we studied the adaptation of a number of clones in each species of paramecia to the gradually increasing salinity of the medium. For each clone we recorded at the start its initial resistance to salinity in the standard culture fluid, before the beginning of experiments with acclimatization. For this purpose infusoria were at first equalized in respect to nutritive conditions. Fifty individuals of each clone were placed for a day in 5 cm.³ of the nutritive medium. On the following day infusoria were taken from such a preparatory culture and placed by groups of four individuals into each depression slide. To each group were added 8 drops of saline medium in varying concentrations (0.3, 0.4, 0.5 per cent, etc.) without food. The cultures were left at 25°C., and on the following day the number of individuals was counted. Experiments with each clone were repeated twice and yielded a curve relating the number of survived individuals with the salinity of the water. Fig. 1 represents such a curve for the line 12 b_1 of *P. caudatum* before its acclimatization to increased salinity. In experiments with *P. caudatum* 245 such curves were obtained. The initial resistance to salinity in each clone was measured by the concentration of salts killing 50 per cent of the individuals per day (i.e. leaving still alive 2 individuals out of 4). This value was read from the concentration-toxicity curve, and

in the case of the line 12b₁ of *P. caudatum*, shown in Fig. 1, it makes 0.47 per cent.

The same procedure was employed at different stages in the process of acclimatizing infusoria to increased salinity. The resistance to salinity measured at that time evidently exceeded the value of initial resistance. The difference between the subsequent and initial resistance to salinity in each clone gives the value of its adaptive modification. To eliminate fluctuations due to possible other causes, determinations of resistancies in the initial and acclimatized cultures of paramecia were usually made simultaneously. Experiments with various clones were performed under perfectly identical environmental conditions, and hence differences between clones in the values of

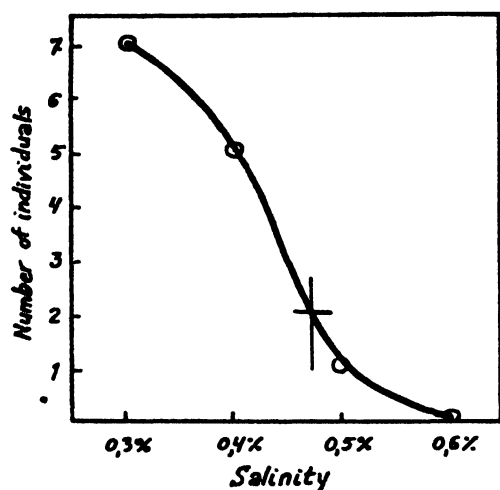


FIG. 1. RESISTANCE TO SALINITY BEFORE ACCLIMATIZATION IN THE CLONE 12b₁ OF *P. CAUDATUM*

both initial resistance and adaptable modification were only due to inherent, genotypic causes.

If in the work with *Paramecium caudatum* the salinity of the medium is increased slowly, and later it ceases to increase, so that in 50 days the concentration of salts attains only 0.36 per cent, a peculiar phenomenon is observed. It appears as if physiological organization of paramecia approaches a kind of steady state, as far as we record in this case the "constancy of the total value of adaptation", which is shown in Fig. 2 and Table 1.

On the abscissae of Fig. 2 we placed the values of initial resistance to salinity in various clones of *P. caudatum*. On ordinates are put the values of adaptive modification of resistance in the same

clones. It is clear that the sum of these two characters (initial adaptation plus adaptive modification)—or in other terms, the value of the total resistance, that is to say, the total adaptation to salinity—represents a constant amount in the most diverse clones. This total resistance is expressed by the following salinities: 0.688, 0.689, 0.685 and 0.690 per cent (Fig. 2).

Hence it is possible to conclude that a casual genotypic increase or weakening of initial adaptation is by no means simply added to the value of adaptive modification. It is instead observed that clones of paramecia, which are genotypically

TABLE 1

Resistance to salinity in various clones of *P. caudatum* before and after slow acclimatization to 0.36 per cent of salinity

Average data of two series of experiments. Resistance is expressed by the concentration of salt killing 50 per cent of the individuals per 24 hours. The test was made on the 50th day from the beginning of the experiment.

NUMBER OF THE CLONE	INITIAL RESISTANCE	SUBSEQUENT RESISTANCE	ACQUIRED RESISTANCE OR ADAPTIVE MODIFICATION
3a ₁	0.37	0.68	+0.31
3a ₂	0.43	0.72	+0.29
3b ₁	0.48	0.66	+0.18
3b ₂	0.45	0.66	+0.21
12a ₁	0.40	0.66	+0.26
12a ₂	0.46	0.71	+0.25
12b ₁	0.46	0.71	+0.25
12b ₂	0.44	0.72	+0.28
30a ₂	0.48	0.69	+0.21
31b ₂	0.53	0.69	+0.16
32a ₁	0.48	0.69	+0.21
32b ₂	0.43	0.67	+0.24

weak at the start, compensate this weakness by increased capability for adaptive modification. At the same time those clones of paramecia which are genotypically strong in the initial resistance possess but weak adaptability. In consequence of such a situation their initial strength is nullified, so far as it does not offer any advantage in respect to the total adaptation.

This conclusion is made here with some reservation, as far as the necessity of certain corrections will be evident from further experiments. Let only two points be noted at this time. (1) From the physiological point of view, a strong negative

relation of initial adaptation to adaptive modification shows that these two characters are not independent, but are instead due to activity of one and the same physiological system capable of yielding only a certain fixed amount of adaptation. When much material is spent upon initial inherent adaptation, only a little can be added to it by the way of adaptive modification. (2) From the evolutionary point of view, it is important that no simple summation of adaptability with the initial adaptation is possible.

Negative relation between initial resistance to salinity and the value of adaptive modification were also observed in experiments with *Paramecium bursaria*. Various exconjugant strains of this species were gradually acclimatized to 0.21 per cent of salinity (through the stages of 0.007,

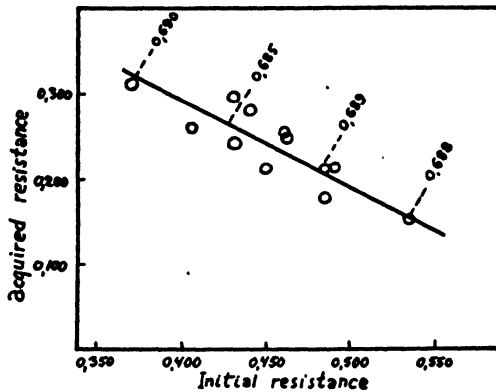


FIG. 2. THE RELATION OF ACQUIRED RESISTANCE TO INITIAL RESISTANCE TO SALINITY IN VARIOUS CLONES OF *PARAMECIUM CAUDATUM*. The case of slow acclimatization.

0.07, and 0.14 per cent). Their resistance was tested 45 days after the beginning of the experiment, and the results obtained are given in Table 2.

It is clear that clones 1a₁, 1b₁, S and R possess lower initial resistance as compared to 2a₁ and 2b₁, but at the same time they exceed these latter clones in respect of capability for adaptive modification. Adaptability in the inherently weaker clones is so strong, that in respect of total resistance to salinity after acclimatization (i.e. by the total adaptation) these clones even overtake initially stronger strains. It follows, therefore, that the relation of initial adaptation to adaptive modification is actually negative, but that the constance of the total amount of adaptation is only approximate and by no means absolute. To this point we shall return later.

The relation of adaptability to adaptation is very interesting, and it certainly should be studied also in animals other than Protozoa. (Adaptive modification under increased salinity in a clone of vegetatively reproducing infusoria biologically corresponds to ontogenetic adaptability in multicellular animals.) One is inclined to expect theoretically the following three possibilities: negative relation, positive relation, and no relation at all between both variables. At present, however, quantitative data in this field are practically non-existent, and only one other zoological example is known to the writer.

Kalabukhov (1937) studied adaptations in the blood of forest mice to a mountainous mode of living. In high altitudes oxygen tension is lower than on the plain. It is well known that blood of

TABLE 2

Resistance to salinity in various clones of *P. bursaria* before and after acclimatization to 0.21 per cent of salinity

Resistance is expressed by the concentration of salt killing 50 per cent of the individuals per 24 hours. Each figure is the average data of two series of tests with four experiments in each series.

NUMBER OF THE CLONE	RESISTANCE BEFORE ACCLIMATIZATION	RESISTANCE AFTER ACCLIMATIZATION	ADAPTIVE MODIFICATION
1a ₁	0.267	0.400	+0.133
1b ₁	0.266	0.400	+0.134
2a ₁	0.293	0.380	+0.087
2b ₁	0.278	0.337	+0.059
S	0.264	0.405	+0.141
R	0.262	0.400	+0.138

mammals is very sensitive to the decreased oxygen tension. In order to provide the tissues with oxygen under conditions of oxygen-deficiency in the atmosphere, the number of erythrocytes and haemoglobin-content of the blood are increased. At this time only the variation in the number of erythrocytes will be considered.

Kalabukhov studied several species of mice belonging to the genus *Apodemus*, including *A. sylvaticus*, *A. flavicollis*, and *A. agrarius*. Experimental transportation of mice from the plain to the mountains has shown that in high altitudes the number of erythrocytes in the blood of *Apodemus sylvaticus* increases considerably in comparison with the initial number. This species acclimatizes well in high altitudes, in spite of the deficient atmospheric pressure. The behavior of the species

Apodemus agrarius is quite different. When simultaneously transported from the plain to the mountains, the number of erythrocytes in the blood of this species increases so insignificantly that it does not provide the tissues with a proper supply of oxygen. Due to such a weak capacity for adaptive modification, this species cannot survive transportation to high altitudes, and rapidly dies out. Table 3 gives some comparative data on the alteration of the number of erythrocytes in *Apodemus sylvaticus*, *A. agrarius*, and *A. flavicollis*.

It is easily seen that when the initial number of erythrocytes is great, this character does not give any significant adaptive modification. Such is the case of *Apodemus agrarius*. In the experiments

perishes. In *A. sylvaticus*, however, the number of erythrocytes is far remote from this maximal possible value. Hence this species possesses sufficient potentialities for adaptive modification.

In conclusion it should be noted that it is not the total number of erythrocytes in the blood, i.e. the total value of adaptation, but evidently only the magnitude of the adaptive modification which is important for natural selection in a population of mammals subject to a mountainous climate. Without a powerful adaptive modification in the number of erythrocytes, the increased demand of the tissues for oxygen cannot be supplied, however considerable might be the initial number of erythrocytes of the animal.

TABLE 3

Number of erythrocytes in millions per 1 mm.³ in the blood of various species of mice on the plain and after their elevation to high altitudes

From Kalabukhov (1937)

SPECIES	INITIAL NUMBER OF ERYTHROCYTES ON THE PLAIN	THE FINAL NUMBER OF ERYTHROCYTES IN HIGH ALTITUDES	THE INCREASE OF THE NUMBER OF ERYTHROCYTES (ADAPTIVE MODIFICATION)
I. Transportation to high altitudes			
1. <i>Apodemus sylvaticus</i>	8.6	9.4	+0.8
2. <i>A. agrarius</i>	9.3	9.4	+0.1
II. Prolonged action of artificially decreased atmospheric pressure			
1. <i>A. sylvaticus</i>	8.4	9.2	+0.8
2. <i>A. agrarius</i>	10.6	9.0	-1.6
3. <i>A. flavicollis</i>	7.5	9.5	+2.0

with artificially reduced atmospheric pressure the number of erythrocytes in this species even somewhat decreases. However, when the initial number of erythrocytes is small, the magnitude of its further adaptive increase is rather considerable (*A. sylvaticus* and *A. flavicollis*). The final number of erythrocytes—or, in other terms, the total value of the adaptive feature of organization—again appears to be more or less constant within the limits of the genus *Apodemus*. One again comes across strong negative relation of adaptation to adaptability, which is represented graphically in Fig. 3. One gets the impression that there exists a certain maximal possible number of erythrocytes in the blood of mice of the genus *Apodemus*. The species *A. agrarius* possesses on the plain this maximal number. At the time of elevation to higher altitudes, the number of erythrocytes has, so-to-say, nowhere to expand, the adaptive modification is not formed, and this species

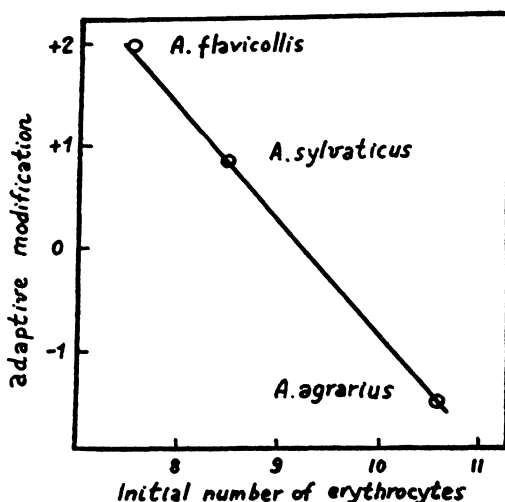


FIG. 3. THE RELATION OF ACQUIRED NUMBER OF ERYTHROCYTES TO THE INITIAL NUMBER OF ERYTHROCYTES ON THE PLAIN IN VARIOUS SPECIES OF MICE BELONGING TO THE GENUS *Apodemus*

THE NON-CONSTANCY OF TOTAL ADAPTATION
IN SOME ADAPTIVE CHARACTERS

It has already been remarked that the constancy of the total value of adaptation in various clones of Protozoa is approximate and not absolute. When the salinity of the medium had for some time ceased to increase, and the process of adaptation of the physiological organization of the paramecia approached to a kind of the steady state, it is true that total salt-resistance in diverse clones of infusoria is approximately constant. Experiments show, however, that in the course of active adaptation of paramecia to the increasing salinity of the medium, a characteristic deviation is observed from the constancy of the total resistance.

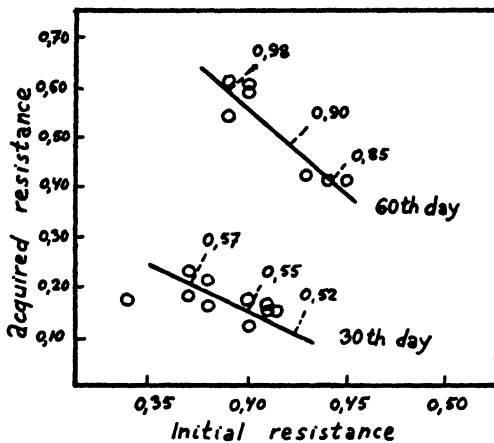


FIG. 4. THE RELATION OF ACQUIRED RESISTANCE TO INITIAL SALT RESISTANCE IN VARIOUS CLONES OF *PARAMECIUM CAUDATUM* ON THE 30TH AND 60TH DAY FROM THE BEGINNING OF THE EXPERIMENT

If in the work with *Paramecium caudatum* the salinity of the medium is gradually increased for a month up to 0.36 per cent, and then maintained at this level for 20 days more, the subsequent test will yield an approximate constancy of resistance in diverse clones, as shown in Fig. 2. If, however, the course of adaptation is more rapid, so that paramecia are tested on the 30th day from the beginning of the experiment at 0.36 per cent of salinity, and on the 60th day at 0.60 per cent of salinity, one observes the relation represented in Fig. 4. The relation of initial resistance to salinity of a given clone of paramecia to the amount of adaptive modification acquired by it is again negative. However, the sum of these two characters (i.e. the total adaptation) is no longer even

approximately constant in various clones. Rather peculiar is the gradual increase of total resistance from the right to the left clones in Fig. 4 (0.52, 0.55, 0.57; again 0.85, 0.90, 0.98). In other words, clones initially weak in resistance acquire such powerful adaptive modifications that their total resistance to salinity outrun that of inherently stronger strains. This means that inherently weaker strains, by means of adaptive modification, are "over-strengthened." A similar picture was observed in *P. bursaria* (Table 2).

Let us attempt to appreciate these observations from the viewpoint of the hypothesis of hereditary fixation of adaptive modifications by means of natural selection of genocopies. Which clones will survive in the natural selection? It is true that natural selection requires special analysis, and this will be presented at length in the following section of this paper. At present let us only discuss briefly the advantages and disadvantages of the various clones. One is inclined to admit that in the adaptation to the increased salinity of the medium the leading part is played by the total resistance to salinity, or in other terms, by the total value of adaptation. Which part of this total resistance is inherent and which acquired is probably unimportant. It is further apparent that natural selection in the mixed cultures of paramecia will operate throughout the adaptive process. The natural selection of stronger strains certainly will not wait the attainment of the steady state, when the adaptation is in the main completed and various clones of paramecia approximately equalized in their properties. In the course of adaptation to increased salinity, the total resistance is not the same in infusoria of various clones. The strongest total resistance will be possessed by those clones which are weak at the start but powerfully adaptable (Fig. 4). All other conditions being equal, it is these strains which will survive the natural selection.

Natural selection for great total adaptation in the gradually changing environment will consequently lead to survival of strains with genotypically weakened initial adaptation and genotypically enhanced adaptive modification. This conclusion from experimental data directly contradicts the above-mentioned hypothesis of the hereditary fixation of adaptive modifications by the means of natural selection of genocopies. Natural selection under our conditions increases adaptive modifications at the expense of reducing

the strength of inherent initial adaptations resembling them.

The conclusion just arrived at means simply that in the mechanism of adaptation of *P. caudatum* to the increased salinity of the medium will take place the selection for adaptability. Such a situation is only possible because the adaptive modification makes here the lion's share of the value of total adaptation. The part played by the value of initial resistance to salinity is relatively small. A combination of the strong adaptive modification with the slight initial resistance appears to be more advantageous in respect to the total resistance than a combination of the weak adaptive modification with the strong initial resistance. At the same time, such combinations as that of strong adaptability with the genotypically strong initial adaptation turn out to be impossible for some physiological reasons.

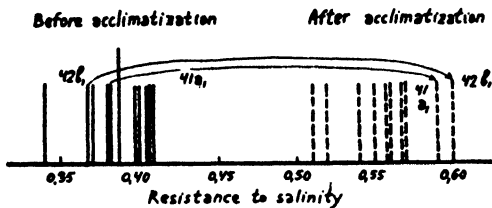


FIG. 5. INITIAL (CONTINUOUS LINES) AND ACQUIRED (DOTTED LINES) RESISTANCE TO SALINITY IN VARIOUS CLONES OF *PARAMECIUM CAUDATUM*. Resistance is expressed by the concentration of salt killing 50 per cent of the individuals per 24 hours.

Fig. 5 shows graphically the resistance to salinity in various strains of *Paramecium caudatum* before and after rapid acclimatization by them to the salinity of 0.36 per cent. The test was made on the 30th day from the beginning of the experiment. One is impressed by the fact that inherent diversity in the initial resistance to salinity is relatively weak, and it is much overlapped by the capability to form adaptive modifications which is peculiar to all the strains, and hence by inherent diversity in the adaptability which here arises.

The same picture is observed in experiments with 20 diverse strains of the other species, *Paramecium aurelia*. For the purpose of acclimatization these were at first placed in 0.1 per cent of salinity, three days later in 0.2 per cent and so on, until the concentration of salts attained 0.4 per cent. Under these conditions paramecia were cultivated for a week and then their salt resistance was deter-

mined by the usual method. Fig. 6 shows the data obtained, which are closely similar to those recorded for *Paramecium caudatum*.

The story heretofore reported shows that powerful capability for the formation of adaptive modifications is a necessary prerequisite condition for natural selection for adaptability. But the very feature of adaptability has behind it some historical grounds. It closely depends upon natural conditions of habitat of a given species. For example, Gause (1939) and Smaragdova (1940) recorded that *Paramecium caudatum* and *P. aurelia* more readily adapt themselves to the increased salinity than does *P. bursaria*. The two former species easily acclimatize themselves to 0.4–0.6 per cent of salinity while at the same time the increase of salinity over 0.21 per cent is usually fatal for *P. bursaria*. It is probable that weak adaptability of *P. bursaria* to increased salinity

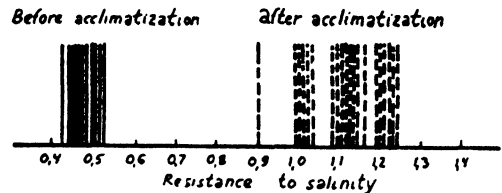


FIG. 6. INITIAL (CONTINUOUS LINES) AND ACQUIRED (DOTTED LINES) RESISTANCE TO SALINITY IN 20 VARIOUS CLONES OF *PARAMECIUM AURELIA*. Resistance is expressed by the concentration of salt killing 50 per cent of the individuals per 24 hours.

is due to the fact that in the peat bogs, which are the natural habitats of this species, the concentration of electrolytes is very low.

It would be interesting to analyze the mechanism of the adaptive process in the case when the part played by adaptive modification in the total value of adaptation is rather low, and when the leading rôle belongs to the value of the casual initial resistance. With that purpose we turned to the action upon Protozoa of such chemical factors as were probably never met by them in their natural habitats. In this case strong adaptability is not to be expected.

Such new factors are presented by the action on Protozoa of various drugs. Quinine and arsenic preparations are widely used to cure diseases caused by pathogenic Protozoa. They are repeatedly introduced into the infected organism, and it is often observed that parasites become acclimatized to their action and are no longer

destroyable by the drugs in usual doses. It was Ehrlich who recorded this process in his work with arsenic compounds. Whether this acclimatization of pathogenic Protozoa to the action of drugs is due to the natural selection of the more resistant strains of the parasite in the course of the treatment, or whether it depends on the formation of adaptive modifications on the part of the parasites, is not known.

We attempted to elucidate such relations by studying the action of quinine upon various strains of *Paramecium caudatum*. Paramecia were acclimatized to living in dilute solutions of quinine hydrochloride added to their standard nutritive fluid. In the first month the concentration of quinine was brought to 0.0036 per cent (through the intermediary stages of 0.0009, 0.0018 and

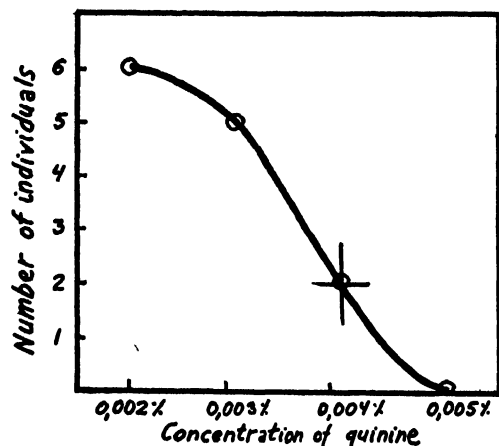


FIG. 7. RESISTANCE TO QUININE AFTER ACCLIMATIZATION TO 0.0036 PER CENT SOLUTION IN THE CLONE 42a₁ OF *P. CAUDATUM*

0.0027 per cent) and in the second month to 0.0063 per cent (through intermediary dilutions of 0.0045 per cent and 0.0054 per cent). (The dynamics of acclimatizing paramecia to quinine was equalized with that employed in the experiments with salts. The concentration of 0.0036 per cent of quinine and 0.36 per cent of salt are approximate resistancies of non-adapted individuals of *P. caudatum*. Such concentrations of chemicals in the nutritive medium were reached in a month, through three equally distributed intermediary stages.) The method of testing the initial and acquired resistance to quinine in each separate clone was identical with that employed in experiments with acclimatization to salinity. Fig. 7 shows a typical curve relating the number

of survived individuals with the concentration of quinine in the clone 42a₁ of *P. caudatum* acclimatized to 0.0036 per cent of quinine. The resistance was again measured by the concentration of quinine killing 50 per cent of individuals per 24 hours.

Fig. 8 shows the distribution of resistances to quinine before and after acclimatization to 0.0036 per cent solution in various clones of *P. caudatum*. The test was made on the 30th day from the beginning of the experiment. Fig. 8 shows that casual inherent diversities between separate clones of paramecia in respect of quinine resistance before acclimatization are evidently rather considerable as compared to the slight capability to the adaptive modification, which is still present.

The mechanism of acclimatizing paramecia to quinine is evidently essentially different from their acclimatization to increased salinity. Which

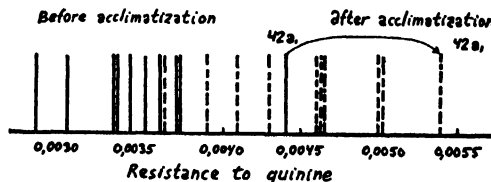


FIG. 8. INITIAL (CONTINUOUS LINES) AND ACQUIRED (DOTTED LINES) RESISTANCE TO QUININE IN VARIOUS CLONES OF *PARAMECIUM CAUDATUM*

Resistance is expressed by the concentration of salt killing 50 per cent of the individuals per 24 hours.

strain, in the case of quinine, will possess the greatest total resistance after acclimatization? Table 4 shows that it is the strain 42a₁. Although this strain is, by the magnitude of its adaptive modification, much behind many of the other lines, its casual initial resistance is very strong. Due to this fact the total resistance of the strain 42a₁ turned out to be ahead of the other strains.

In the case of quinine, adaptability will evidently not play any leading rôle for natural selection. This is again illustrated by Fig. 9. The most useful appears to be the combination of the powerful initial adaptation with the relatively moderate adaptive modification. Its total resistance attains 0.0054. Combinations of weaker initial adaptations with the more powerful adaptive modifications yield smaller values of the total resistance (0.0050, 0.0047, 0.0044). Combinations of powerful initial strength with the strong adaptability are again absent.

Summarizing, it could be stated that the acclimatization of paramecia to quinine is essentially different from their acclimatization to salinity. In the case of quinine, the conditions are favorable for the selection of the casual initial strength of resistance accompanied by the relatively moderate adaptability. At the same time, in the acclimatization of paramecia to increased salinity, a selec-

TABLE 4

Resistance to quinine in various clones of *P. caudatum* before and after acclimatization to 0.0036 per cent solution

Resistance is expressed by the concentration of quinine killing 50 per cent of the individuals per 24 hours. Average data of three series of experiments.

NUMBER OF THE CLONE	RESISTANCE BEFORE ACCLIMATIZATION	RESISTANCE AFTER ACCLIMATIZATION	ADAPTIVE MODIFICATION
41a ₁	0.0033	0.0046	+0.0013
41a ₂	0.0034	0.0050	+0.0016
41b ₁	0.0037	0.0046	+0.0009
41b ₂	0.0028	0.0043	+0.0015
42a ₁	0.0044	0.0054	+0.0010
42a ₂	0.0036	0.0041	+0.0005
42b ₁	0.0030	0.0050	+0.0020
42b ₂	0.0033	0.0036	+0.0003
44a ₁	0.0037	0.0046	+0.0009
44a ₂	0.0035	0.0039	+0.0004

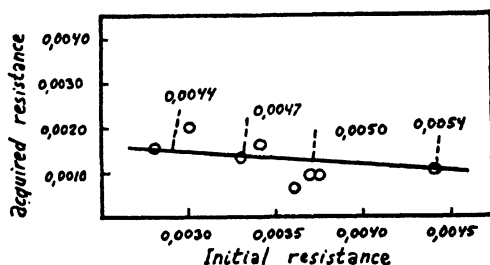


FIG. 9. THE RELATION OF ACQUIRED RESISTANCE TO INITIAL RESISTANCE TO QUININE IN VARIOUS CLONES OF *PARAMECIUM CAUDATUM* ON THE 30TH DAY FROM THE BEGINNING OF THE EXPERIMENT

tion is inevitable for the strong adaptability accompanied by the weak initial strength. Neither in the first nor in the second case did we come across the summation of the strong adaptation with the profound adaptability.

NATURAL SELECTION FOR ADAPTABILITY

We have heretofore assumed as self-evident that the value of the total resistance of a clone of

infusoria to some unfavorable environmental conditions is wholly responsible for the survival or disappearance of this clone in the process of natural selection. But it is clear that this assumption should be analyzed more carefully.

At present we possess a very delicate and conclusive method of demonstrating natural selection of some specific clones in the mixed populations of infusoria. The method is founded upon the properties of the so-called mating types of infusoria, discovered recently by Sonneborn (1937) and Jennings (1938). In the case of *Paramecium bursaria* the individuals of any given clone will not conjugate with the individuals belonging to the same clone, or to another clone if this is of the mating type identical with theirs (e.g. of the type I). At the same time they will readily conjugate with individuals of a clone which belongs to the antagonistic mating type II. The conjugation is preceded by the specific reaction of agglutination. If one mixes two clones belonging to different mating types, the individuals almost immediately agglutinate or become clumped into dense groups, which later desintegrate into conjugating pairs (Jennings, 1939). Let us now consider the case of a mixed population consisting of two clones, belonging to type I and type II, respectively. This population acclimatizes itself to the unfavorable environmental conditions. After a while one can exactly see whether both mating types of paramecia survived in the mixed culture, or whether one of them disappeared in the process of natural selection. For that purpose one must take a sample of a mixed population in appropriate physiological condition (i.e. not overfed), and add to it, in one experiment, some new individuals belonging to the type I, and in the other, of type II. If in this procedure individuals of type I will not cause agglutination of infusoria, but such an agglutination will be caused by the added individuals of the type II, this would mean that individuals of the latter type disappeared from the mixed culture. Agglutination reaction makes visible the survival or disappearance of mating types. The species *Paramecium bursaria* is particularly appropriate for such a work, because the clones of this species in continued vegetative reproduction retain for many months their specific mating types (Jennings, 1939). The situation in *P. aurelia* and *P. caudatum* is less fortunate.

In the experiments with *P. bursaria* four clones numbered 1a₁, 1b₁, 2a₁ and 2b₁ were used. The division-rate per day in these clones in the standard medium of Beers at 25°C, in the average of two series of observations, is as follows: 2.94; 3.57, 3.13, 4.23. Their initial and acquired salt resistance is given in Table 2. The following mixtures yielded immediate conjugation: 1a₁ + 1b₁; 2a₁ + 2b₁; 2a₁ + 1a₁.

Conjugation was induced in the medium of Beers, and populations of conjugants from each mixed culture were gradually acclimatized to the salinity of 0.21 per cent for a period of 45 days, through the intermediary stages of 0.007, 0.07, and 0.14 per cent of salinity. At the same time the cultivation of mixed populations of conjugants was continued in the initial medium of Beers. Every three to four days paramecia living in mixed cultures were re-inoculated. For that purpose a part of the culture (about 100 individuals out of 1000) was transferred to 5 c.c. of the newly made nutritive medium. The same was the method of cultivation of separate clones. It is clear, however, that in the mixed culture must go on the process of natural selection of those clones which acclimatize and multiply more rapidly, and by this increase their relative numbers in the mixed population through a series of consecutive re-inoculations of the culture.

The test of composition of mixed cultures was made on the 45th day after the beginning of the experiment. For that purpose we mixed in the dense suspension 50 individuals from the mixed culture with 50 individuals from one of the pure strains entering into the composition of the mixture. On the following day the number of conjugants was counted. For the control, 100 individuals from the mixed culture alone were similarly isolated. The results of analysis are given in Table 5.

When the clone 1a₁ is added to a mixed culture (1a₁ + 1b₁) or to (2a₁ + 1a₁), conjugation is observed immediately. This means that the clones with the mating type of 1a₁ disappeared in the course of cultivation from both mixed cultures cultivated in the initial medium of Beers as well as acclimatized to increased salinity.

Natural selection in the mixture 2a₁ + 2b₁ is somewhat different. In the saline medium the clone of the type 2b₁ disappeared, but in the medium of Beers it was the clone 2a₁, which perished

in the mixed culture. This conclusion was confirmed by a great number of repeated tests.

The very fact of disappearance from mixed cultures of one of two mating types is interesting and suggestive. It shows that vigor or weakness of paramecia is closely bound with their mating type, so that disappearance of the weak individuals represents at the same time the disappearance of one of two antagonistic mating types. It is to be remembered that mixed cultures were started by conjugating individuals. This conjugation, as every hybridization generally, must have produced numerous new combinations of hereditary characters. If the physiological vigor or weakness of

TABLE 5
Analysis of composition of mixed populations of Paramecium bursaria by the mating types technique

NAME OF THE CULTURE ANALYZED	NAME OF THE CLONE ADDED FOR ANALYSIS	CONJUGATION
Salinity 0.21 per cent		
1a ₁ + 1b ₁	1a ₁	+
1a ₁ + 1b ₁	1b ₁	—
2a ₁ + 2b ₁	2a ₁	—
2a ₁ + 2b ₁	2b ₁	+
2a ₁ + 1a ₁	2a ₁	—
2a ₁ + 1a ₁	1a ₁	+
Initial medium of Beers		
1a ₁ + 1b ₁	1a ₁	+
1a ₁ + 1b ₁	1b ₁	—
2a ₁ + 2b ₁	2a ₁	+
2a ₁ + 2b ₁	2b ₁	—
2a ₁ + 1a ₁	2a ₁	—
2a ₁ + 1a ₁	1a ₁	+

infusoria were distributed by conjugation at random and independently of the mating type, both types should later be partially eliminated from the mixed culture, and total extinction of only one of them could not have been recorded.

At the same time these experiments represent a direct proof of strong natural selection among closely related clones in the mixed populations of infusoria. In what the weakness of perished clones consists is rather clear. The salt resistance of the clone of the mating type 2b₁, which disappeared in the course of acclimatization to salinity, is lower than that of the survived clone 2a₁ (Table 2). The division rate per day of the clone 1a₁

(2.94), which disappeared in the medium of Beers, is lower than the division rate of the better fitted clone 1b₁ (3.57).

In a number of other experiments natural selection in the mixed cultures of infusoria was studied by a different method. We simultaneously ac-

climatized to the increased salinity of the medium various isolated clones, and also cultures consisting of all these clones combined together. We have always observed that salt resistance of individuals from a mixed culture approaches that of the most resistant strains entering into its composition. It was hence concluded that these most vigorous

strains survived in the mixed culture, and that the whole population consists of them alone.

Tables 6 and 7 show the data obtained. In *P. aurelia* the average resistance to salinity of 20 separately acclimatized clones attains 1.129. If

TABLE 6

Resistance to salinity in various clones of *P. aurelia* before and after acclimatization to 0.4 per cent of salinity

Resistance is expressed by the concentration of salt killing 50 per cent of the individuals per 24 hours. The test was made on the 20th day from the beginning of the experiment.

NUMBER OF THE CLONE	RESISTANCE BEFORE ACCLIMATIZATION	RESISTANCE AFTER ACCLIMATIZATION	ADAPTIVE MODIFICATION
1a ₁	0.470	1.140	+0.670
1a ₂	0.422	1.080	+0.658
1b ₁	0.500	1.145	+0.645
1b ₂	0.477	1.090	+0.613
2a ₁	0.525	1.165	+0.640
2a ₂	0.458	1.230	+0.772
2b ₁	0.480	1.240	+0.760
2b ₂	0.485	1.100	+0.615
3a ₁	0.480	1.195	+0.715
3a ₂	0.465	1.120	+0.655
3b ₁	0.520	1.015	+0.495
3b ₂	0.520	1.230	+0.710
4a ₁	0.520	0.900	+0.380
4a ₂	0.540	1.210	+0.670
4b ₁	0.507	1.130	+0.623
4b ₂	0.510	1.105	+0.595
5a ₁	0.550	1.160	+0.610
5a ₂	0.430	0.990	+0.560
5b ₁	0.455	1.125	+0.670
5b ₂	0.430	1.200	+0.770
Average of 20 isolated clones	0.487	1.129	+0.642
Mixed population No. 1	0.487	1.230	+0.743
Mixed population No. 2	0.487	1.245	+0.758

TABLE 7

Resistance to salinity in various clones of *P. caudatum* before and after rapid acclimatization to 0.36 per cent of salinity

The test was made on the 30th day from the beginning of the experiment.

NUMBER OF THE CLONE	RESISTANCE BEFORE ACCLIMATIZATION	RESISTANCE AFTER ACCLIMATIZATION	ADAPTIVE MODIFICATION
41a ₁	0.40	0.57	+0.17
41a ₂	0.38	0.59	+0.21
41b ₁	0.41	0.57	+0.16
41b ₂	0.41	0.56	+0.15
42a ₁	0.41	0.56	+0.15
42a ₂	0.40	0.52	+0.12
42b ₁	0.37	0.60	+0.23
42b ₂	0.34	0.51	+0.17
44a ₁	0.38	0.54	+0.16
44a ₂	0.37	0.55	+0.18
Average of 10 isolated clones	—	0.557	—
Mixed populations	—	0.620	—

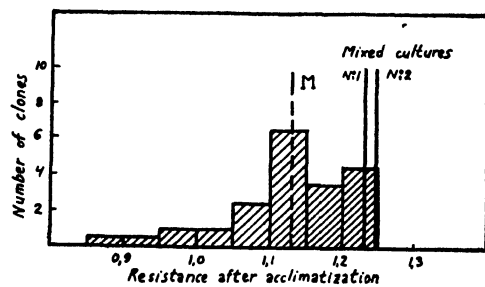


FIG. 10. VARIATION IN SALT RESISTANCE AFTER ACCLIMATIZATION IN 20 SEPARATE CLONES OF *P. AURELIA*. M is the average salt resistance of 20 isolated clones. Continuous vertical lines show the resistance of mixed cultures.

climatized to the increased salinity of the medium various isolated clones, and also cultures consisting of all these clones combined together. We have always observed that salt resistance of individuals from a mixed culture approaches that of the most resistant strains entering into its composition. It was hence concluded that these most vigorous

there were no natural selection at the time of acclimatization of mixed cultures, such would be also the resistance of a mixed population, so far as at the beginning of the experiment it consisted of members of 20 separate clones mixed in equal numbers. The observation shows, however, that the

resistance of an acclimatized mixed population is greater and makes 1.230 and 1.245. This is also evident from Fig. 10, which shows the variation in salt resistance after acclimatization in 20 separate clones of *P. aurelia*. The resistance of individuals from a mixed culture approaches that of the several most vigorous clones. It is hence evident that these clones alone survived natural selection in a mixed population. The same story is repeated in the cultures of another species, *P. caudatum*. Table 7 shows that the average salt resistance of 10 isolated clones of this species is 0.557, but the

vived in the mixed culture. The names of the survived clones being thus known, it was easy to calculate their average initial resistance to salinity. In a similar way we calculated the average adaptive modification for all the isolated clones of paramecia, and on the other hand, the average adaptive modification (from the figures of isolated clones) of those which remained in the composition of the mixed culture.

The results of such calculations for populations of *P. caudatum* are given in Table 8. It is clear that the average initial salt resistance of those

TABLE 8
Resistance to salinity and quinine solutions in Paramecium caudatum and P. aurelia

TIME IN DAYS FROM THE BEGINNING OF ACCLIMA- TIZATION	RESISTANCE AFTER ACCLIMATIZATION			RESISTANCE BEFORE ACCLIMATIZATION			ADAPTIVE MODIFICATION		
	Average for isolated clones	Average for mixed population	Increase of mixed population in per cent	Average for isolated clones	Average for clones sur- vived in mixed culture (by calcula- tion)	Increase of mixed population in per cent	Average for isolated clones	Average for clones sur- vived in mixed culture (by calcula- tion)	Increase of mixed population in per cent
<i>P. caudatum: Salt resistance</i>									
30	0.567	0.625	+10	0.384	0.375	-2	0.183	0.238	+30
25	0.523	0.595	+14	0.352	0.345	-2	0.171	0.210	+23
27	0.583	0.640	+10	0.428	0.432	+1	0.155	0.182	+17
56	0.954	1.000	+5	0.438	0.424	-3	0.516	0.610	+18
61	0.893	0.960	+7	0.393	0.392	0	0.500	0.528	+6
<i>P. aurelia: Salt resistance</i>									
20	1.129	1.237	+9.5	0.487	0.485	-0.4	0.642	0.737	+15
<i>P. caudatum: Resistance to quinine solutions</i>									
33	0.00496	0.00510	+3	0.00387	0.00386	0	—	—	—
25	0.00411	0.00445	+8	0.00321	0.00330	+3	—	—	—
27	0.00449	0.00540	+20	0.00321	0.00343	+7	—	—	—
28	0.00452	0.00500	+11	0.00347	0.00358	+3	—	—	—
58	0.00981	0.01020	+4	0.00379	0.00405	+7	0.00602	0.00543	-11

resistance of individuals from a mixed population attains 0.620.

An attempt was made to investigate the point whether the clones that survived possess strong initial salt resistance, or whether they exceed others in the capability for adaptive modification. We have consequently performed the following calculations. In each series of experiments the resistance of an acclimatized mixed population was compared with the resistance of all separately acclimatized clones. From such a comparison it was determined which clones most probably sur-

clones which survived in mixed cultures is somewhat below the average initial resistance of the whole group of clones. On the other hand, the adaptive modification of survived clones much exceeds the average adaptive modification of all the clones. A similar picture is recorded for *P. aurelia*.

On the basis of the data given in Table 8 it is possible to conclude that in the acclimatization of paramecia to the gradually increasing salinity of the medium, natural selection of the clones actually occurs with powerful adaptability but rela-

tively weak initial adaptation. Natural selection contributes to further increase of adaptability by casual inherent variations in that direction. In this way the preliminary conclusions of the previous section of this article made on the ground of study of total salt resistance, and of its fractionization into constituent adaptability and adaptation in various isolated clones, are entirely confirmed by the direct study of natural selection in mixed cultures.

What, however, occurs in the case of adaptation of *P. caudatum* to dilute solutions of quinine? Table 8 shows that there is a clear selection in mixed cultures for great total resistance, so far as the resistance of the acclimatized population exceeds the average resistance of isolated clones. In distinction from adaptation to salinity, a great initial resistance of a clone to the action of quinine guarantees to it some advantage in natural selection. This conclusion directly follows from the fact that the average initial resistance of the clones survived in mixed cultures exceeds the average resistance of all the isolated clones. On the other hand, the magnitude of adaptive modification of survived clones is by 11 per cent behind that of all the clones studied. This again confirms the conclusions of the previous section.

SUMMARY

The relation of adaptability to adaptation within the population of one and the same species is negative, i.e. the stronger the initial inherent adaptation the weaker is the adaptability, and vice versa. This conclusion follows from observations on unicellular organisms, but it was shown to agree well with the data obtained in the work with other animals.

In the adaptation of animals to gradually changing environmental conditions, the magnitude of genetic diversity in the adaptability of different individuals in a population is very important as compared to the magnitude of diversity of the same individuals in their inherent initial strength. In the case of adaptation of *P. caudatum* and *P. aurelia* to the increasing salinity of the medium, the larger part of total adaptation is due to adaptability. The clones that survived in mixed cultures are here weak in the initial strength but powerfully adaptable. On the other hand, in the case of acclimatization of *P. caudatum* to dilute solutions of quinine, adaptability is low as compared to magnitude of inherent diversities of various clones in the initial resistance. It is consequently the profound initial strength which is important for the survival of a clone in the mixed culture. The survivors here are well adapted but poorly adaptable.

LIST OF LITERATURE

- BARBARIN, V. 1938. Factors determining the balance of fat and glycogene in *Paramecium caudatum*. *Biol. Zhurn.*, 7: 391 (in Russian with French summary).
- CALKINS, G. N. 1902. Marine Protozoa from Woods Hole. *Bull. U. S. Fish. Comm.*, Vol. 21.
- FINLEY, H. E. 1930. Toleration of fresh water Protozoa to increased salinity. *Ecology*, 11: 336.
- FLORENTIN, R. 1899. Études sur la faune des mars salées de Lorraine. *Ann. Sc. Nat. Zool.*, T. 10.
- FRISCH, J. A. 1935. Experimental adaptation of fresh-water ciliates to sea water. *Science*, 81: 537.
- FRISCH, J. A. 1939. The experimental adaptation of *Paramecium* to sea water. *Arch. Protistenkd.*, 93: 38.
- GAUSE, G. F. 1939. Studies on natural selection in Protozoa. I. The adaptation of *Paramecium aurelia* to the increased salinity of the medium. *Zool. Zhurn.*, 18: 631 (in Russian with English summary).
- . 1940. On the importance of adaptability for natural selection. *Zhurn. gen. Biol.*, 1 (in Russian with English summary).
- , and N. P. SMARAGDOVA. 1939. Studies on natural selection in Protozoa. II. A comparative investigation of adaptation of *Paramecium caudatum* to the increased salinity of the medium and to quinine solutions. *Zool. Zhurn.*, 18: 642 (in Russian with English summary).
- GOLDSCHMIDT, R. 1938. Physiological Genetics. McGraw-Hill Book Company, New York.
- JENNINGS, H. S. 1913. The effect of conjugation in *Paramecium*. *Jour. Exp. Zool.*, 14: 279.
- . 1938. Sex reaction types and their interrelation in *Paramecium bursaria*. *Proc. Nat. Acad.*, 24: 112.
- . 1939. Genetics of *Paramecium bursaria*. I. Mating types and groups; their interrelations and distribution; mating behavior and self sterility. *Genetics*, 24: 202.
- , RAFFEL, D., LYNCH, R., and T. M. SONNEBORN. 1932. The diverse biotypes produced by conjugation within a clone of *Paramecium aurelia*. *Jour. Exp. Zool.*, 62: 363.
- KAHL, A. 1928. Die Infusorien (Ciliata) der Oldesloer Salzwasserstellen. *Arch. Hydrobiol.*

- KALABUKHOV, N. I. 1937. On the reaction of some species of rodents living on the plain upon the decreased atmospheric pressure. *Zool. Zhurn.*, 16: 483 (in Russian with English summary).
- QUENNERSTEDT, A. 1865. Bidrag till Sveriges Infusorie-fauna. *Acta Univ. Lund. Mathem.-naturw. Abt.*
- LEVANDER, K. M. 1894. Materialien zur Kenntnis der Wasserfauna in der Umgebung von Helsingfors. I. Protozoa. *Acta pro Fauna et Flora Fennica*. Vol. 12.
- LOEFER, J. 1939. Acclimatization of fresh-water ciliates and flagellates to media of higher osmotic pressure. *Physiol. Zool.*, 12: 161.
- LUKIN, E. 1936. On the causes of substitution of modifications by mutations in the process of organic evolution from the viewpoint of the theory of natural selection. *Trans. Kharkov Univ.*, No. 6 (in Ukrainian).
- PEARL, R. 1939. The Natural History of Population. *Oxford*.
- RAFFEL, D. 1930. The effect of conjugation within a clone of *Paramecium aurelia*. *Biol. Bull.*, 58: 293.
- SCHMALHAUSEN, J. 1938. Organism as a Whole in the Individual and Historic Development. *Moscow* (in Russian).
- SMARAGDOVA, N. P. 1940. Studies on natural selection in Protozoa. III. Natural selection in populations of *Paramecium bursaria*. *Zool. Zhurn.*, 19 (in Russian with English summary).
- SMITH, J. C. 1904. A preliminary contribution to the protozoan fauna of the Gulf Biological Station. *Rep. Gulf Biol. Sta., (New Orleans)* 2: 43.
- SONNEBORN, T. M. 1937. Sex, sex inheritance and sex determination in *Paramecium aurelia*. *Proc. Nat. Acad.*, 23: 378.
- YOCOM, H. B. 1934. Observations on the experimental adaptation of certain fresh-water ciliates to sea water. *Biol. Bull.*, 67: 273.





THE PHYLOGENY OF SOCIAL NESTING HABITS IN THE CROTOPHAGINAE

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INTRODUCTION

THE reproductive behavior of birds is based on the construction and maintenance of a nest. Normally a male and a female select a nest site and build a complicated structure for raising the young. Although nesting behavior is not limited to birds, nevertheless the habits reach their climax in variety and complexity in this class. The variations in nesting behaviors are innumerable and frequently demonstrate phylogenetic sequences.

The Crotophaginae, one of the six subfamilies of Cuckoos, has developed the unusual habit of building communal nests in which several females lay eggs. The phylogeny of this remarkable system of raising young is the subject of this paper. The family Cuculidae as a whole shows a tendency to develop peculiar breeding habits. Of the approximately 200 species of Cuculidae, about 80 are parasitic (Makatsch, 1937), representing two of the six subfamilies. This parasitism is found in several stages of development. Some species perhaps are just starting on the road to parasitism; for example the eggs of the Yellow-billed Cuckoo (*Coccyzus americanus*) have been found in the nests of at least 12 species of birds (Herrick, 1910). Other species are always parasitic. The least specialized of these lay eggs in the nests of numerous species. In other cases, as represented by the European Cuckoo (*Cuculus canorus*), the birds are individually host-specific (Friedmann, 1928a). Thus individuals of the species each parasitize particular host species, although in the same region other individuals may lay eggs in nests of other host species. The climax has been reached by certain species, such as *Eudynamis honorata*, which parasitize only one species in a region. The Crotophaginae, however, instead of developing parasitism as other cuckoos have done, have specialized in the direction of social nesting habits.

Before considering the background of the subject let us now proceed to review briefly the subfamily Crotophaginae. This group of birds consists of the monotypic genus *Guira* and the genus *Crotophaga*, the latter represented by three species: *major*, *sulcirostris*, and *ani*. The distribution of the subfamily extends from Rio Negro in Argentina north throughout the West Indies to Florida and throughout Central America to Texas. The birds have noisy, ostentatious habits and everywhere are abundant and conspicuous members of the avifauna.

At this point, in order to orient the reader, a brief description of the behavior of the species is inserted. All four species of the subfamily possess the same general behavior patterns and for the purposes of this paper may be described in general terms. The species prefer fairly open and moist habitats and are conspicuous in behavior, all using loud notes and making no effort to conceal themselves. The birds associate in flocks of about a dozen individuals, spending the days together and sleeping in the same tree. Each flock defends its territory by fighting. At the breeding season members of the flock cooperate in the building of a single nest in which several females may lay eggs. The males assist in the construction of the nest and in the care of the young. After the breeding season the young stay with the flock for a variable length of time and may help in the care of the next brood, and may even breed with the colony the next season. During the non-breeding season the birds tend to congregate in moist areas where insects, their favorite food, are most abundant. The composition of the flock varies over a period of time; a bird may leave, or, after a period of fighting, join the group. In connection with the flock behavior are many calls and actions which are of value to the group as a unit.

These species, whose behavior has been briefly

described, show the development of a system of social nesting. The phylogeny of breeding habits within a group of animals is usually obscured by the extinction of some of the species which represent stages in the development. This situation makes it necessary to speculate and to reason from analogy. In some cases, however, the evolution of behavior may be traced through a small group of closely related species, as Friedmann (1929) has done in the Cowbirds. The *Crotophaginae* is another group of birds in which we are able to trace the steps in the evolution of a peculiar type of breeding habits, as this paper endeavors to show. The phylogeny of other groups of animals has been studied from the behavioristic viewpoint, for example, the ants in Wheeler's classic studies (1923, 1928). Emerson (1938) analyzes the nests of termites to trace the behavioristic and evolutionary sequences.

In discussing the evolution of any particular condition in animals it is customary to seek "causes" which determine the "effect." This principle of Cause and Effect, however, encounters numerous philosophical difficulties and in biology is further complicated by the simultaneous action of several factors. For the purposes of this paper, then, we shall not discuss any cause of the development of social nesting habits but merely state the conditions under which the breeding behavior evolved. From the evidence here presented it will be seen that social nesting habits are the logical outcome of these conditions and that, in this case, were any one of the several factors lacking, the habits probably could not have developed. These same habits, of course, probably could have resulted from a different evolutionary history. In addition it should be noted that the unusual social nesting, as found in the behavior of *Crotophaga ani*, is the result of a combination of situations, no one of which is in itself unusual, but all of which when combined, permit the social nesting. These various conditions may be regarded as conducive to the development of the habit. Throughout this paper examples of other species will be cited to show that none of the particular behavior patterns is unique but that all occur in one or more groups of birds.

Before considering in detail the behavior of the birds, it is desirable to discuss some features of their anatomy and then their geographical distribution. In their internal anatomy the various species show no significant differences. Of the

external features the development of the keel on the bill in the members of the group is spectacular. *Guira* has a typical cuculine bill but the genus *Crotophaga* has developed a large thin keel on the bill. In *Crotophaga major* the keel extends one-half way to the tip of the bill and in *C. ani* the keel is high and thin, extending to the tip. In *C. sulcirostris* the keel is grooved. In coloration *Guira* is again obviously the most closely allied to the other cuckoos. Its body feathers are white but the tail, wings, and head are streaked with brown and some black, giving the appearance of a brown bird; a notable feature is the crest of feathers on the head. The genus *Crotophaga* is uniformly black, with a different amount of blue iridescence in the plumage of each species. Both *major* and *ani* have a remnant of the crest on the head as shown by a few feathers which are slightly longer than the others. The evidence from the external features indicates that *Guira* is positively the more primitive genus and that within the genus *Crotophaga*, *C. ani* is probably the most evolved. The development of the bill and the black color and the reduction of the crest are evidence of evolution within the group.

Concerning the geographical distribution of the subfamily it may be said that the group is either very young or more probably has been unable to spread very far because of a lack of ability to adapt itself to colder climates. *Guira* is found in Brazil and Argentina. *C. major* is found from northern Argentina through Brazil to Panama. *C. sulcirostris* occurs on the west coast from northern Peru through Central America to Texas. *C. ani* is the most widespread, occurring from northern Argentina to Yucatan and Florida and also through the West Indies. This distribution suggests a gradual dispersal from the highlands of Brazil.

With this introduction as a background we shall now consider the phylogeny of behavior. A preliminary section brings together notes on comparative behavior within the subfamily and reference to problems of discrimination and to "releasers". The stages in the evolution of social nesting are next analyzed. The development occurs at three levels, represented by the species (1) *Guira guira*, (2) *Crotophaga major*, (3) *C. ani* and *C. sulcirostris*. The primary factors conducive to the development of social nesting habits are (a) modification of territorialism (b) aberrant breeding, (c) the type of habitat. These three levels of development will be analyzed in a separate section for each of the

above factors. Finally there is a discussion of the phylogeny of behavior within the group and its general relation to social parasitism.

COMPARATIVE BEHAVIOR OF THE CROTOPHAGINAE

The author has had the opportunity to observe the same species in very distant parts of its geographical range. The study of a species in one particular locality may be misleading because of certain local mannerisms. Since studies of the same species of bird, carried out by the same observer in widely separated places, are rare, these data are considered worth reporting in some detail. The following notes are recorded in order to afford a comparison of the habits of *Crotophaga ani* in British Guiana and in Argentina with the habits of the species in Cuba (Davis, 1940a).

In British Guiana each flock strictly maintains a territory exactly as in Cuba. However, the vegetation of certain areas permits an apparent variation in behavior. For example, along the Abary River are occasional open areas of savanna, always surrounded by rain forest. Many of these areas are not large enough for more than one group of *C. ani* and hence in these cases no territorial fighting can appear between groups, for there are no neighbors with whom to fight. However, the occasional stranger is driven out by fierce fighting. Another modification of the territory is that *C. major* is permitted to share the territory. Certainly there is competition for food between the two species.

The colonies found in Guiana were smaller than many found in Cuba. For example, on July 13, 1939, I found a colony with five adults and a nest containing one young bird. Another colony containing six adults had three young, two weeks old. A month later I found a colony with four adults (two females, one male, one of unknown sex) and a nest containing four young ready to leave the nest. It should be noted that in these groups probably only one female laid in each nest, for in no case were there more than six young birds.

Observations on *C. ani* were made also near Saladas in the Province of Corrientes in Argentina. Here the species is not sufficiently abundant to show territorialism clearly. One group of birds (12), including some juveniles, inhabited a particular area, near a small marsh. Also another colony, consisting of three adults, had a nest with three young. Several times an individual or two of *Guira guira* came near and even perched in the

same tree with an individual of *C. ani* without causing the latter to show defense of the territory. Again it is of importance that, as in British Guiana, the territory is not defended against a species so closely related, both taxonomically and ecologically. In summary it may be said that in the general activities, as well as in the particular habits mentioned above, the behavior of *C. ani* is the same in British Guiana, in Argentina, and in Cuba.

Correlation of anatomy and behavior

An interesting relationship between anatomy and behavior is shown in the Crotophaginae. It is considered that a display behavior develops before the particular structure used in the display; the wing marks of the ducks are the classic example. Lorenz (1935) describes the uses in herons of certain structures for elaborate display. Chapman (1935) calls attention to the fact that a manakin of Brazil (*Chiroxiphia*) has an elaborate dance but no special structure such as is found in other members of the family. A corollary of this principle is that the structure remains after the behavior has disappeared. The development of the crest in the Crotophaginae may be an example of this corollary. The large crest of *Guira* is raised in alarm and also when the alarm rattle is given. *C. ani* has no such alarm note but has retained some feathers on the head which are somewhat longer than the nearby ones. This little crest is never used. This retention of a structure after the behavior is lost follows naturally from the fact that the structure is developed after the behavior.

Conspicuous buccal markings are found in the nestlings of *Guira* and also of *C. major*. In *C. ani* these markings are present but much less distinct.

Social behavior

The similarity of the call notes throughout the group is of interest. *C. ani* has the most varied vocabulary and is the most social. The alarm call of *C. major* greatly resembles the rattle alarm of *Guira*. But the most noteworthy is the resemblance of the flight flock call, the note used to notify other members of the group of the movements of one individual. In *Guira* the note is weak and indistinct. In *C. ani* the note is nearly identical in pitch but is very loud and harsh. The use is the same in both cases. The flight flock call of *C. sulcirostris* is of the same pattern. The

notes used in mating are in the whole group a uniform series of soft whines.

The Crotophaginae agree with most other birds in having two calls to indicate danger. The 'alarm' call notifies the members of the group of a walking enemy or suspicious situation. The 'danger' call is used to warn of an approaching hawk or other flying predator. Many species of birds have this separation by call of the types of danger. Makkink (1936) found in the Avocet (*Recurvirostra avocella*) that there was one call for the chief enemy, the gulls, and another for all other enemies.

Social behavior has nearly always developed coincident with an extension of the time the young remains with the adults (cf. ants, wasps, and humans). In the Crotophaginae, however, there is no evidence that social nesting or flock behavior is a result of this extension. Nevertheless it is of great interest that the young of one brood have been observed feeding the young of the second brood in *C. ani* (Davis, 1940a) and also in *C. sulcirostris* (Skutch, 1935). Furthermore, as Skutch points out, it is not unusual for unmated birds of many species to assist at the nest. Skutch (1940) found that the young of some wrens remain with the adults and even feed the young of the succeeding brood. According to Leach (1925), the young California Woodpeckers (*Balanosphyra formicivora*) also feed the young of the second brood. Thus we see that the cohesion of the family in several species of birds is the result of communal nesting, but not the cause.

The type of peck order or social hierarchy is of great importance in a social group. In the Crotophaginae no suitable behavior was found which could be used to rank the birds. While feeding, contests for juicy morsels occasionally occurred but showed no peck order. Lorenz (1938) points out that when there is a rigid peck order in colonial birds only one pair can raise young. In the Jackdaws (*Coleus monedula*) this situation is overcome by the fact that the despot pecks only the nearest in rank. In the Crotophaginae if a peck order occurs, a similar situation probably obtains.

Discrimination

Under the term, discrimination, many problems of animal behavior are grouped. The problem in general is to analyze a series of behaviors to determine which characteristics of the stimulating object act on which sense organs of the reacting ani-

mal to influence a subsequent behavior. In birds the stimulating characteristics are usually some morphologic or behavioristic element. The reacting organs are generally visual or auditory. In this paper is discussed the evidence concerning the discrimination of three of the many objects occurring in the bird's life, namely, the sex-partner, other individuals of the species and the boundaries of the territory.

The evidence concerning the discrimination of the sex-partner is meager. The problem is to find out what features of a bird are the clues which make possible the determination of the sex. In appearance the sexes are identical in all species of Crotophaginae except that the male is larger. Experiments with dummy birds were performed on *Crotophaga ani*. These dummies were museum skins arranged to resemble a live bird. In most cases the birds attacked the dummies as if they were live invaders of the territory. Sometimes after the dummy had been in one place a long time the owners of the territory ignored it. Decoy (live) birds, placed in a trap in order to catch the birds, were treated exactly like strangers and killed in a short time. Young birds, however, were ineffective as decoys because the adults did not respond in either a helpful or an antagonistic manner. The above evidence suggests that the Crotophaginae belong to the "labyrinth fish" type of mating reaction according to the classification of Lorenz (1935). In this category the display of the male develops into fighting except when the stranger shows female behavior. However, the assignment of the Crotophaginae to this category depends on insufficient evidence. In no case was "female behavior" observed to result in a cessation of fighting. This is, of course, not contradictory evidence but merely lack of evidence.

An important modifying condition is the relationships imposed on the individuals by the flock organization. It seems likely that an individual must be admitted to the flock before it can be eligible for pairing. If this is true then all the fighting observed was in reference to membership in the flock and none in reference to the sex-partner. If this is the case then we must admit that we have no evidence as to the method of discrimination of the sex-partner.

Another problem is to determine which sense modalities are used in discrimination of other members of the species or of other species. There is no doubt that each member of the flock knows

individually every other member of the group. (Cf. Davis, 1940a, 1940b, 1941a.) The problem is to determine which sense modality is used in this discrimination. A natural experiment occurs in the presence of the species *Ptiloxena atroviolacea*, an entirely black Icterid about one-third smaller than *Crotophaga ani*. *C. ani* persecutes this species and drives it from the territory. The behavior towards *Ptiloxena* consists of the same series of patterns used against an intruder of the *Crotophaga* species. Another black species in the region, the rare *Corvus nasicus*, was seen only once and at that time was being persecuted by a group of *Crotophaga ani*. *Holoquiscalus niger*, another Icterid, was not observed to be persecuted—a situation probably due to the ecological separation of the habitats. As further evidence it may be noted that, according to the natives of Cuba, albino birds live with the flock in a normal manner; the writer never observed an albino bird. The above facts, showing that black birds of other species in addition to dummy birds are attacked, suggests that the discrimination is by means of vision and not by audition. That the auditory sense modality is used in certain species is shown by the work of Noble, Wurm, and Schmidt (1938) who found that herons (*Nycticorax nycticorax*) recognize their sex-partners by voice. Experiments with mirrors (Davis, 1940a) show that individuals of *Crotophaga ani* do not recognize themselves but fight against their own image. This evidence eliminates the olfactory sense modality, already improbable, from consideration.

Now, having outlined the evidence and suggested the conclusion that these birds utilize the visual sense modality for the discrimination of other individuals, it is necessary to consider what characteristics of the stranger stimulate the reacting bird. In general the problem is to determine whether behavior or physical appearance is the basis of discrimination. The evidence from the reactions to *Ptiloxena* and to the dummies suggests the conclusion that strange birds are recognized not by their behavior but by their appearance. Were behavior the means of discrimination only birds which behaved in a certain manner would be attacked. But birds are driven out which resemble *Crotophaga* in appearance although their behavior has no resemblance to that of an invading bird. The tolerance of *C. major* by *C. ani* in Guiana is an apparent exception which may be explained by assuming that the *ani* have learned

to recognize the *major* as individuals. It must be remembered that for the moment we are concerned with the recognition, not of the sex-partner, but of a stranger. Nevertheless, the data pertaining to the recognition of a sex-partner are useful in an attempt to analyze the situation in the *Crotophaginae*. Referring to other species, the Kingbirds (*Tyrannus tyrannus*) (Davis, 1941b) drive from their territory birds of various species whose behavior varies greatly and whose only common characteristic is an appearance different from that of the female. Tinbergen (1939) refers to errors of identification by the Snow Bunting (*Plectrophenax nivalis*). In these cases the behavior of the female is of the type which should indicate that she belongs in the territory. However, the male does not recognize the physical features of his mate and starts to fight until her features are recognized. Tinbergen also found that the male Bunting requires some time to learn to recognize his mate and until that time threatened her whenever she came into his territory. Lorenz (1935) states that a young bird must learn a certain number of characteristics of the parent before becoming able to recognize and thus not threaten it. The Jackdaw is a species which certainly does recognize the individuals of the flock by appearance, not by behavior. Also, Lorenz points out that the social life of birds differs from that of insects because there is a personal recognition of the individuals in the group. Noble and Vogt (1935) found that some species (*Agelaius phoeniceus* and *Geothlypis brachydactyla*) which differ in the plumage of the sexes, recognize the female by physical appearance. Noble (1936) carried the work further and found that the 'moustache' of the Flicker (*Colaptes auratus*) was necessary for sex recognition. In contrast, other species, which frequently are identical in the plumage of both sexes, recognize individuals by behavior (Noble and Vogt, 1935). Lorenz (1935) found that young herons recognize their parents by behavior. This evidence from other species suggests the possibility that even in the *Crotophaginae* the initial recognition of a stranger is by means of the behavior of the individual. This suggestion is supported by the work of Noble and Curtis (1939). In the Jewel Fish (*Hemichromis bimaculatus*) the sex of a stranger is recognized initially by behavior but after pairing the mates recognize each other by individual characteristics of appearance. In the *Crotophaginae* it is difficult to determine

exactly what the behavior might be which would indicate that a strange bird is not a member of the group. However, the lack of knowledge of the territory may be noticable to the owners. Then on close inspection the owners may see that the bird is a stranger and drive it out. Also there is the possibility that a lack of certain positive behavior patterns identifies a bird as being a stranger.

In addition to the question of discrimination of individual birds there is the problem of the discrimination of the boundaries of territories. The birds remain so strictly in their own territory that there must be an exact knowledge of the very trees and shrubs which mark the edge. In Cuba it was most amusing to watch the members of a group follow the electric mowing machine which the birds had learned was a source of an easy meal of insects. Each group followed the machine to the exact boundary of the territory but did not trespass beyond, in spite of the strong attraction of food. The birds clearly recognized the individual trees or bushes which marked the boundary.

Members of the *Crotophaginae* are able to recognize individuals which seem identical to the human observer. Yet these same birds are unable to recognize that such a bird as *Ptiloxena* is of another species. These facts suggest a conflict in the interpretation. It seems likely that this apparent discrepancy may be resolved by a consideration of the probability that birds learn one or two special characteristics of each individual bird and unless these are present, consider the individual to be a stranger. Lack (1939) found that only a few characteristics of the English Robin (*Erithacus rubecula*) were required to cause the owner of the territory to attack a dummy. In humans the ready deception accomplished with disguises shows how very few marks we need to recognize our friends.

Releasers

The fact that a certain few characteristics are used to discriminate among individuals of the same species is further evidence that social behavior is largely controlled by specific combinations of special stimuli. These stimuli are anatomical structures or behavior patterns which are in themselves unusual or are combined in unusual behavior sequences. Such sequences are of so improbable a nature that they do not occur in the experience of the species except under the proper circum-

stances. Therefore, the automatic and inflexible response to the stimulus occurs only at the proper time. Such stimuli or series of stimuli have been called releasers (Von Uexkill and Lorenz) or sign-stimuli (Russell, 1934). The studies of the *Crotophaginae* have provided examples of several releasers which it is proposed to mention at this time. On one occasion a dove (*Zenaidura macroura*) fluttered off her nest, performing typical injury-feigning, right into the midst of a group of anis. The birds at once acted toward the dove as if it were a wounded individual of their own species. They crowded around the dove, fluttered and used a chuckle note. They did not use the 'conk', a note uttered while attacking a stranger. As another example the mutual preening has many of the characteristics of releasers. The moment that the bill of one bird touches the neck of its neighbor the neck is raised and the feathers fluffed out. This occurs in all species of the subfamily. This action may be no more than a simple reflex. The feeding of the young of the second brood by the young of the first brood is probably a social companion action. It is possibly released not by the young in the nest but by the action of the other adults.

The imperfections of releasers are probably as informative as the perfections. Witness the interesting conflict between the response to the alarm call and the strict observance of the boundaries of the territory. When the investigator disturbed a nest, the alarm call was used and the birds from nearby groups came near but they never passed the boundaries of the territory although it was obvious that the alarm call was a strong attraction. As another example of an imperfection of releasers, individuals of the Mockingbird (*Mimus polyglottos*) were able to mimic the alarm call and released the alarm behavior of the nearby anis. This observation shows that the discrimination was not very exact for even the writer could distinguish after short practice between the mocker and the true alarm note.

MODIFICATION OF TERRITORIALISM

The concept of territorialism has developed from attempts to interpret various types of fighting behavior of animals. This concept has had great heuristic value and in addition has clarified the interpretation of the behavior of many species. In other species (Cowbirds) the analysis of the manifestation of territorialism has suggested a

possible course of phylogeny of behavior. It is now proposed to present the relation of territorialism to the phylogeny of behavior in the Crotophaginae and then take up the modifications of the concept as suggested by the behavior of the Crotophaginae. This chapter emphatically is not a critique of the theory of territorialism or of the many criticisms of the concept.

In all the species of the subfamily the colony owns a territory which consists of two distinct parts. One of these is a clump of trees for sleeping and the other an area of fairly open land for feeding. From this territory, in general, other members of the species are expelled. Among the species, however, certain differences exist. *Guira guira* defends its territory only slightly; numerous intrusions are permitted, although on some occasions birds are violently driven out. The colony lives in a large but nevertheless definite area, and, since it is defended, it can be called a true territory. The important point is that within this colonial territory one or two pairs may have their own small territories. One or more pairs may separate from the colony and build a nest, setting up around this nest a territory from which intruders are expelled. However, the defence of this small territory is not vigorous and in many cases other birds of the colony use the nest, thus producing a communal nest. This weak defence of the territory has thus permitted social nesting.

In *Crotophaga major* the development of social nesting has continued. The birds remain in pairs, all cooperating to build one nest in which several females lay eggs. Probably not all females lay eggs at the same time and also probably a single pair does occasionally build a nest and raise young. The colony defends the territory for the whole group, although weakly. Lack of defence is probably more apparent than real and depends on a mutual understanding. Such behavior occurs in other species. For example Ryves (1929) found that in Redshanks (*Totanus totanus*) "once an individual territory has been definitely secured by a pair of birds and approved by the other pairs of the same species, a distinct mutual understanding if not friendship developed among them."

In *Crotophaga ani* the communal nesting has reached its climax. Each colony defends its territory most aggressively and without exception attacks strangers. The marital relations are very flexible. Polygamy is the general rule for it is certain that in some cases polyandry occurred and

in others polygyny prevailed. Yet in some groups monogamy was strict and there was no dissension among pairs. In one case a pair created a territory and defended it alone. Wetmore (1927) cites two instances in which he believed that a single pair built a nest.

Crotophaga sulcirostris is apparently at the same level of development as *C. ani*. The observations of Skutch (Bent, 1940) indicate that the birds have the same marital relations as does *C. ani*.

The phylogenetic development of social nesting coincides with the disappearance of territorial defence by the pair and the appearance of territorial defence by the colony. Other species have developed social breeding habits of several types, which can be roughly contrasted with the stages in the Crotophaginae. Several examples of these species will now be cited to illustrate for comparison the three levels in the development of crotophaginine social nesting.

At the phylogenetic level of *Guira* may be cited the numerous species which spend most of the year in flocks but separate out into pairs for breeding. A few examples will suffice. Tinbergen (1939) found that Snow Buntings separated from the flock to acquire territory. The Oyster-catcher (*Haematopus ostralegus*) (Huxley, 1925) has a nesting territory but a common feeding ground. The coveys of Bob-white (*Colinus virginianus*) (Errington, 1933) break up in April to pair for breeding. These examples show that a weakened territorial defence by a pair under certain conditions could permit the flock to remain together and lead to communal nesting.

Another bird shows the behavior at the level of *C. major*. In the species *Yukina bruneiceps* (Timaliidae), according to Yamashima (1938), "several pairs of birds join in building one nest." His data for four nests show that four or six birds, laying two or three types of eggs, composed each flock. *Corydon* (de Schaunessy, 1928) may have similar habits. In addition a comparison with the Jackdaw (Lorenz, 1931, 1938) and the Rook (*Corvus frugilegus*) (Yeates, 1934) is instructive. In these species, although there is a colonial territory, the strict maintenance of pair territories has prevented social nesting. Some Magpies (*Pica*) (Linsdale, 1937) live in similar colonies. The Weaver Finch, *Philestariius*, (Friedmann, 1930) nests in colonies and the colony defends a territory. Some colonial birds have no colonial territory, as the Oropendolas (*Zarhynchus wagleri*) (Chapman,

1928). Thus a colonial territory does not necessarily result in communal nesting unless, among other contributing factors, the pair territory is weakened.

At the level of the development of *C. ani* and *C. sulcirostris* the breeding of the California Woodpecker may be mentioned. The woodpeckers live in colonies and several pairs cooperate in excavating a nest hole and raising the young (Leach, 1925; Ritter, 1938). Two Australian genera, *Corcorax* and *Pomatorhinus* (Friedmann, 1925) are reputed to nest communally. Thus at each level in the phylogeny of the Crotophaginae, examples from other groups may be cited, each with a different modification or weakening of the territorialism of the pair.

Breakdown of territorialism in the Crotophaginae

Before analyzing the factors responsible for the breakdown of territorialism within the Crotophaginae, it is desirable to note the assumption that territorialism was originally present in the group. Territorialism is now considered to be a widespread phenomenon in the vertebrate classes. Breder (1936) has summarized the behavior of many fishes (Centrarchidae) and Noble (1938) and Noble and Curtis (1939) have analyzed the relation of sexual selection to territorialism. In those fishes which build nests the male guards the nest site. When the female arrives and copulation occurs, the eggs are deposited. The male in many species guards the eggs and then the young until they are able to fend for themselves. The defence in these species has the characteristics of avian territorial defence and can be differentiated from sexual fighting as such. In the Amphibia data indicate that the male commonly has a calling and mating station but as yet these data are insufficient to be certain that this is analogous to the territories of birds. For lizards the work of Evans (1936, 1937, 1938) and Evans and Clapp (1940) has shown that the species *Anolis carolinensis* maintains a territory in accordance with the characteristics of avian territories. For birds, the evidence is overwhelming that most species are territorial. The reviews of Nice (1933) and Lack and Lack (1933) indicate the extent of the behavior. For the Cuculidae in particular, Makatsch (1937), Friedmann, (1928b) and Davis (1940c) indicate that territorialism is nearly universal within the group. Chance (1922) found that the female European Cuckoo will lay in an unusual fosterer's

nest rather than leave her territory. However, there are records of two females using the same territory (Gosnell, 1932). Among the African Cuckoos, Friedmann (1928a) found that many parasitic species have territories which are dependent upon the availability of nests to parasitize. However, *Lampromorpha* has a faulty defence of territory and *Eudynamis* has lost the territorial instinct. Therefore, since territorialism occurs in most other cuckoos, we would seem justified in assuming that it was originally present in the Crotophaginae. The manner in which the behavior patterns of territorialism were weakened and modified may now be considered.

Several factors probably have contributed to the breakdown of territorialism for the pair. The first is that sexual fighting (fighting in relation to the sex-partner) is absent or extremely weak in the whole subfamily Crotophaginae. This situation may have permitted freer relations between the various members of the colony and a loosening of the sexual bond. As to the origin of the lack of sexual fighting it may be suggested that a contributing factor is the habit of living in colonies, thus producing within the group an individual familiarity which precluded sexual fighting. A second factor which contributed to the breakdown of territorialism is the lack of a song. In most territorial birds song is one of the most effective methods of maintaining a territory. None of the subfamily has any note with the characteristics of song. The possession of a song might have prevented the breakdown of territorialism.

Some observations on the defence of the territory deserve mention. According to the concept, the owners drive out birds of the same species. In the case of *C. ani*, other species, such as *Corvus nasicus*, and an entirely black member of the Icteridae (*Phloxena*) are driven out on all occasions. The defence of territory against the latter species must not be confused with the act of stealing eggs from the nests. The manner of stealing eggs differs in notes, in flight, and in flock behavior from the act of driving a *Phloxena* out of the territory. Although this species is smaller than *C. ani* nevertheless this defence reaction is probably due to an error of identification of the individual. But on the other hand, in British Guiana where *C. ani* is quite as aggressively territorial, *C. major* is permitted to remain in the territory and even sleep within a few feet of some individuals of *C. ani*. *C. major*, to the human observer, more closely

resembles *C. ani* than does *Phloxena* yet apparently there is some feature which serves to distinguish the species. Errors of discrimination are common in other species. Song Sparrows (*Melospiza melodia*) (Nice, 1937), Kingbirds (Davis, 1941b), and the English Robin (Lack, 1939a) frequently drive other species out of the territory. In these cases the behavior is considered to be an exaggerated territorialism.

The observance of territorial boundaries differs among various species of birds. Thus, for example, there is variation in the reactions toward a predator. In *C. ani* when a predator (human, cat) comes to the nest tree of the colony the neighboring birds come near, attracted by the alarm call. But these neighbors do not enter the territory of the disturbed group. The attraction of the alarm call does not override the disposition to remain within their own territory. Some other species, as for example the Willet (*Caloptrophorus semipalmatus*) (Vogt, 1938), will go outside a territory and cooperate in the pursuit of an enemy. Fautin (1940) found that the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), although strictly territorial, cooperated to drive out predators. L. Miller (1930) found that Horned Owls (*Bubo virginianus*) ignored humans when driving an invader out of the territory.

Biological value of territory

The function or biological value of the territory (as distinguished from the psychological cause of fighting) has been discussed at length in the literature. Food supply is the most obvious function. It has been shown (Davis, 1940a) that in *C. ani* the size of the territory of different colonies which contain the same number of individuals varies greatly in the same ecological habitat. Furthermore, in British Guiana, *C. major* may live within the territory of *C. ani* and certainly is a competitor for food. Food, then, is probably not an essential function of territory but an incidental result among these birds. As a matter of fact no function of territory in these species is clearly apparent other than the primary function, the provision of a mating station and nest site. It must be remembered that the function of territory does vary greatly among various species. As an example of the possibilities of variation in the function of territory, Skutch (1931) observed that in the Hummingbird, *Amazilia*, 50 per cent of the nesting failure was due to the birds stealing material from

other hummingbirds' nests. Territorial defense would have prevented this robbery. The function of territory may even change during the year. Thus the Micheners (1935) found that in Mockingbirds (*Mimus polyglottos*) summer territory depended on the nest and was defended only by the male. On the other hand in the winter the male and/or the female may defend a territory for feeding purposes. In January the behavior changes from the winter to summer type of defense. This situation obtains in Shrikes (Laniidae) (A. H. Miller, 1931) and in the English Robin (Lack, 1939a).

These variations in the function of territory emphasize the fact that to be of any value the territorial concept must be sufficiently broad and flexible to describe and integrate the behavior of many species of animals. Meise (1936) shows the great variation in function among different species by classifying territories under various headings: (1) the relation between the size of the territory and area (*Lebensraum*), (2) duration of territory, (3) number of birds using it, (4) biological function. This exhaustive analysis provides a basis for the classification of the territorialism of any particular species. Friedmann (1933) points out that species vary in expressing territorialism in time and space. Both must be considered. As Nethersole-Thompson (1934) suggests, territory operates in relation to the peculiar needs of the species. Even within the same species territorialism may vary. For example, *Larus marinus* (l. c. p. 23) is territorial in some areas and colonial in others. Territorialism is a means to success in reproduction and not an end in itself. The study of the nesting habits of the Crotophaginae furnishes further evidence that territorialism is a variable behavior and can not be rigidly circumscribed by a definition if the concept is to have any usefulness. The patent development within one group of closely related species of a colonial territory from a pair territory, emphasizes the usefulness of an inclusive term.

Several attempts have been made to define strictly territorialism. These definitions are not in terms of function. Every definition presents only one point of view and thus automatically excludes many species. The latest attempt is the definition of Lack (1939a) in which he states that territory is an isolated area defended by one individual of a species or by a breeding pair against intruders of the same species and in which the owner makes itself conspicuous. This definition

suffers from the same drawbacks as any definition of territorialism (cf. Davis, 1940a: 206). It is too narrow and excludes too many species from the concept. Colonial birds, such as the Jackdaws, Crotophaginae, Gulls (Kirkman, 1937), and the California Woodpecker are eliminated. Further, it excludes polygynous species such as *Cassidix* (McIlhenny, 1937), Yellow-headed Blackbird (Fauntin, 1940), *Euplectes* (Lack, 1935), and lizards (Evans, 1938). This definition carries with it the tacit exception that an intruder of the same species which is a potential mate is not driven out and further it does not take into account several birds such as the Chickadee (*Parus atricapillus*) (Odum, 1941) which defend a territory but do not make themselves conspicuous by song or position. For these reasons it seems preferable to align the concept of territorialism with such concepts as 'species' and not try to define it strictly.

It is desirable to call attention to two principal types of fighting. Fighting in reference to the piece of land (territorialism) is the subject of this discussion. The fighting by the Crotophaginae in reference to the sex-partner has not been discussed here for lack of evidence. This lack is probably due to the masking of sexual fighting by territorial fighting. The behavior of the Crotophaginae shows clearly that the defense of territory is a separate element from sexual fighting. Fighting over the sex-partner does not enter into the motivation. The motivation is the defense of the nest and the piece of land. The whole colony defends the territory no matter what the sex of the defenders or intruders may be. It is becoming clear that the separation of the elements of territorial defense and sexual fighting should have been recognized earlier. The behavior of other species shows clearly that there are several causes of fighting among birds. For success in reproduction there are three principal reasons for defending the nest site: (1) Predators must be driven off; (2) A sex-partner must be secured and defended against other members of the species which attempt to obtain the partner; (3) A spot suitable for pairing, for placing the eggs, and for raising the young must be secured. It is proposed to restrict the term territorialism to the last-mentioned type of fighting. The most important separation is the distinction between fighting over the piece of land and fighting in relation to the sex-partner. As examples in other species, Vogt (1938) finds that in the Willet the defense of territory gradually

supersedes the defense of the female as the breeding period advances. Eventually sexual fighting is no longer necessary because territorial defense excludes all males. Defense of territory and of the female are the two causes of strife among Willets and often mask each other. Tinbergen (1939) describes the sexual fighting in the Snow Bunting. After the female arrives fighting increases and the male will fight outside the territory to defend the female. The birds drive away other birds of the same species, but, while the female fights for the male only, the male defends the female and also the territory. In this species territory defense is a behavior of the male only. These considerations demonstrate the variation in the causes of fighting. Territory is a very important cause and has been the subject of this discussion of the Crotophaginae.

It is now important to consider the origin of territorialism. Since the nest is the only factor in the bird's economy which is fixed, it seems likely that the territorial defense originated from the defense of the nest site or mating station. This viewpoint is in agreement with data on other birds and vertebrates. Noble (1940) states that in primitive birds (Night Herons) territories retain their piscine function of being primarily a place where sexual bonds are formed. In fishes (Centrarchidae) the territory is the place where copulation occurs. Secondly, the territory has become the place where eggs are laid and develop. Hubbs and Bailey (1938) found that the Small-mouthed Black Bass (*Micropterus dolomieu*) defends the nest and that copulation occurs only on the nest. Huxley (1914) found that in Great Crested Grebes (*Podiceps cristata*) coition occurs only on the nest. Venables and Lack (1934), in the same species, observed that territorial behavior is clearly correlated with the position of the nest, and again (1936) that territory is associated with the nesting platform. This situation resembles the behavior of fish greatly. Lack (1939b) states that the function of territory in the Blackcock (*Lyrurus tetrix*) is to reduce the amount of interference between males at copulation. Schuz (1936) studying the White Stork states that "one often has the impression that it is first the nest that is defended and second the mate." Friedmann (1929) found that the Cowbird (*Agelaioides badius*) chooses the nest and then the territory. Also (1928a) he finds that in African Cuckoos territory is dependent upon the availability of nests to parasitize. Nethersole-Thompson (1933) in-

cludes interspecific fighting (for example, the fighting between woodpeckers and starlings for a nest-hole) as territorial. The behavior of these species indicates that the place of copulation (nest-site) is the original territory. But among the data contradicting the view is the fact that many highly evolved species choose territory before the nest. In some cases the female builds a nest outside the territory. Lorenz (1938) believes that the territory of the herons has shrunk to small size. Tinbergen (1935) interpreted his data on *Phalaropus lobatus* to indicate that the nest site is not an essential part of territory. Selous (1933) expresses the viewpoint that the territory is symbolical of the female and that the male defends the territory as he would the female. However, this contradictory evidence can be reconciled with the notion that the mating spot is the original territory. A division of nesting activities between the members of the pair can permit great variation in the relations between the mating station (territory) and the nest.

The evidence presented above suggests that the defence of the spot of ground on which sexual bonds can be formed and the nest built is the origin of territory. This viewpoint contains several assumptions. It is assumed that the defense of the piece of land can be extended forward and backward temporally and also can be extended spatially. The forward extension of a behavior pattern is commonplace in the lives of animals. Many species for example, incubate before the eggs are laid (*Ectopistes*, Whitman, 1919). Lack (1940) suggests that feeding the mate during courtship is an extension forward of feeding during incubation. Thus the extension in time of the defense of the nest site and the mating station encounters no difficulties. This viewpoint of the origin also assumes that the bird is able to recognize a potential competitor for the nest site. This recognition permits the explanation of the fact that many species stop active defense of the territory after the nest is built and recognize the territories of other birds by mutual agreement (Nice, 1937). The neighboring birds are known not to be competitors for the piece of land, whereas strange birds are known to be either competitors for the land and/or for the mate.

ABERRANT BREEDING HABITS

As was mentioned in the introduction, the Cuculidae show throughout the entire family a

tendency to have unusual breeding habits. In the Crotophaginae these aberrations have developed into communal nesting. This proclivity is presumably based upon some peculiarity of the endocrine system although at present we know practically nothing about what the exact situation could be; nevertheless several conditions may be mentioned.

Presumably birds, like mammals, may be divided roughly according to the spontaneous or non-spontaneous method of ovulation. It is of course clear that the exact meaning of 'spontaneous' breaks down when courtship is considered. In mammals the term refers to species such as the rat, in which ovulation occurs at regular intervals without external stimulation. Other species (non-spontaneous), such as the rabbit, under natural conditions ovulate only after the stimulation of coition. In birds the external stimulation of coition has been superseded by the more intricate courtship performance. In many cases ovulation can be produced by a very slight external stimulus such, for example, as stroking the neck of pigeons. It becomes very difficult then to determine exactly what species are spontaneous and what are non-spontaneous. Marshall (1936) divides birds roughly into two groups in respect to ovulation; those which ovulate spontaneously and seldom mate for life or have elaborate courtship, and the non-spontaneous ovulators which frequently possess elaborate courtship performances. These generalizations do not hold for Parrots, which mate for life and ovulate spontaneously. The Rhea, which is known to have polygynous nesting habits, probably ovulates spontaneously. Harper (1904) suggests that polygynous birds are spontaneous and that monogamous birds are non-spontaneous. Craig (1913) points out the spontaneous (Phasianidae) and the non-spontaneous (Columbidae) types of ovulation. Allen (1925) although not using the terms spontaneous and non-spontaneous, points out the difference in the type of egg-laying as exemplified by the hen and the pigeon. He further suggests that sight of a nest is the stimulus which causes certain wild ducks to deposit eggs. It must be remembered that there are three distinct phases in the production of an egg. The growth of the egg and follicle is the first stage and apparently is under the control of the follicular stimulating hormone (FSH). The actual ovulation is the second stage and is controlled by the luteinizing hormone (LH). The last stage is

the passage down the oviduct and the actual deposition of the egg in the nest. Just what factors influence this last event is not clear at present. The term spontaneous must be used to refer only to ovulation and not to laying.

There is considerable evidence to indicate that the Crotophaginae as well as the rest of the Cuculiformes are spontaneous ovulators. Farley (1924) reports that a pet which lived in his house, dropped eggs frequently on the floor. The birds drop eggs frequently on the ground even far away from the nest. Although Friedmann (1929) found that Cowbirds frequently drop eggs on the ground, in this case these aberrations are probably the result of social parasitism. The habit of spontaneous ovulation in the Crotophaginae is closely related to the lack of courtship performance. Since the function of courtship behavior is, primarily at least, the stimulation of ovulation, spontaneous courtship and lack of courtship are compatible. In birds such as the Crotophaginae which ovulate spontaneously there is no need or use for courtship. On the other hand, in those species which ovulate non-spontaneously, courtship display does have a use in identifying the sexual ripeness of the individual. Thus Noble (1938) found that in many fishes the display was a means of identifying not the sex but the sexual ripeness of the individual. A further development of this condition is the use of display to stimulate and synchronize the sexes, as Carpenter (1933) found in the pigeons. Huxley (1916, 1921) has suggested that the function of courtship is not selection of a mate but stimulation to copulation. In animals with courtship performances the external stimulus releases the internal endocrine mechanism responsible for ovulation. Craig (1911) found that the pigeon, which normally ovulates after courtship and is considered to be non-spontaneous, will ovulate even if there is no male present, but under these conditions only late in the season. Virgin females may not lay at all without a male. On the other hand, in animals which ovulate spontaneously, the stimulus to ovulation is brought about by an automatic release of the endocrines responsible for it independent of external stimuli. Courtship thus appears to be an external regulator superimposed upon the internal processes.

As a further correlate of spontaneous ovulation and the lack of courtship may be mentioned the lack of pair formation. Courtship, especially

mutual post-ovulatory performances, serves to bind the members of the pair together in some species and to prevent the dissolution of the couple. The courtship performances, either by one of the pair or by both birds, serve to maintain the pair. Thus, in the Crotophaginae, the lack of bonds between the members of the pair and spontaneous method of ovulation are contributing factors permitting communal nesting. It should be emphasized that it is not intended to imply that spontaneous ovulation must necessarily be followed by communal nesting but that spontaneous ovulation permits the lack of courtship and of the bond between members of the pair, thus making possible and contributing to the development of social nesting.

Parenthetically it should be noted that many birds with most elaborate courtship (game birds, birds of paradise, manikins, hummingbirds) do not pair. In these groups the elaborate courtship is necessary to induce copulation.

Number of eggs laid

The two types of ovulation, spontaneous and non-spontaneous, exemplify one phase of the general problem of internal and external control of a neuro-endocrine mechanism. As background for a discussion of another phase of this problem, it is desirable to discuss the number of eggs laid by each female. In both genera of the Crotophaginae the number laid by a female is usually six, although sometimes it is five or seven (cf. Davis, 1940a, 1940b, 1941a). Skutch (Bent, 1940) believes that *C. sulcirostris* lays four eggs, a figure probably too low. Since several females lay in the nest there may be great variation in the number of eggs deposited in one nest. Thus the number of eggs laid by one female cannot be determined by the number in the nest. The number laid can be determined, however, by microscopic examination of the ovaries. The fact that a constant number is laid would suggest that the size of the clutch is fixed by an internal endocrine mechanism. The evidence as reported by Farley (1924), whose pet bird laid eggs for a long period of time, is not described in sufficient detail to be of value in this connection.

That there can be a difference in the method (external or internal) controlling the production of eggs is shown by the consideration of the factors which determine the number of eggs laid. Some birds lay until there is a certain number of eggs in

the nest. The Flicker as reported by Phillips (1887) is the classic example. If eggs are removed from the nest this bird continues to lay until, in one case, as many as 73 eggs have been deposited, although it is possible (in litt.) that several females laid in this one nest. Other species lay only a certain number no matter how the number of eggs in the nest may be manipulated (Davis, unpub., *Larus argentatus*). Craig (1913) recognized these two types of birds and pointed out the Flicker and the pigeon as examples. In the first type (which the author suggests be called indeterminate) the external conditions determine the number of eggs laid. In the second type (determinate) the number is fixed by the internal hypophyseal-ovarian mechanism. The observations of Hann (1937) that in Ovenbirds (*Seiurus aurocapillus*) brooding began after laying the penultimate egg even though 3, 4, 5, or 6 eggs were laid in the clutch, suggests that the brooding impulse may regulate the number of eggs laid. The fact that the Flicker has elaborate courtship (Noble, 1936) suggests that in this species ovulation is non-spontaneous. At present, knowledge is insufficient to state certainly that indeterminate egg-laying is found in birds which ovulate non-spontaneously and that determinate egg-laying occurs in those which ovulate spontaneously.

It is of interest that another bird in which communal nesting has developed, the California Woodpecker, belongs to the Picidae which are prolific egg-layers. The classical example of the Flicker which laid 71 eggs in 73 days shows to what extent the birds can lay eggs. Eggs of various woodpeckers are frequently found in the nesting holes of other birds, and the group as a whole is famous for laying a varying number of eggs. The ducks are also prolific egg-layers and frequently lay in other birds' nests. Allen (1925) has indicated the importance of this habit in the eventual culmination of parasitism in the South American duck *Heteronetta*. Friedmann (1932) lists many species of ducks which have laid eggs in the nests of other species.

The above discussion is concerned with one aspect of the general problem of the interrelations between the nervous and the endocrine systems, namely, the internal or external regulation of the hypophyseal-ovarian mechanism. Another problem concerning the breeding and the relations of the gonads to the nervous system is the fact that, in *C. ani* and others of the subfamily, incubation by

several females starts simultaneously. The individual bird, however, may not have completed its clutch or may have finished laying several days before. It should be noted, however, that in most cases incubation does not start until a few days after the egg-laying has stopped. It seems that continued egg-laying by one bird inhibits the incubation by the other birds. Possibly imitation may be the reason the birds, which have completed ovulation some time previously, start to incubate. It is known in general that the behavior of a bird towards the contents of the nest is dependent upon the contents and can be changed radically by changing the contents of the nest. For example, the substitution of eggs caused *C. ani* to brood for 24 days although the normal length of incubation is about 13 days. A Robin (*Turdus migratorius*) will feed young which are substituted for newly-laid eggs (Davis, unpub.). Contrasting with these species are others which have a fixed duration for each phase of the breeding cycle. Thus the Noddy Tern (*Anous stolidus*) (Watson, 1908) did not change behavior when chicks were substituted for eggs. Apparently this is a species difference in the control of behavior by external and internal stimuli.

Unusual aspects of reproduction

A further factor of unknown significance to the breeding habits is the fact that the Crotophaginae have a continuous molt. In general birds molt just before and/or after the breeding season. It is known that this molt is connected with the endocrine system in several respects. Just what connection, if any, there may be between the continuous molt and the endocrine situation in the Crotophaginae is not clear. It should be noted that other birds such as the Ptarmigan (Salomonson, 1938) have a continuous molt. The observations of the Micheners are of interest in connection with the loss of territorialism as correlated with the molt. These investigators found (1935) that the Mockingbirds maintain territory throughout the year but that there is a slackening of territorial defense during the molt. The English Robin maintains a territory except during the molt (Lack, 1939a).

A word of caution is necessary. Endocrinology is not a panacea for the explanation of all sexual behavior. The task is to find out what relations exist. For example, Lack (1939a) finds that the English Robins establish territories and select

mates in the fall when the gonads are regressed. This indicates that the gonadal hormones at least are not responsible for these particular behavior patterns or that estrin inhibits territorialism in the female when this hormone appears in the spring (cf. plumage in chickens, Domm, 1939). A further complication is the common occurrence of song in the fall. Brewster (1898) observed several species of swallows attempting copulation and carrying mud on August 22, after the migratory flock had formed. These examples indicate the magnitude of the task.

Aberrant breeding habits are frequently connected with an abnormal sex ratio in the population (Mayr, 1939). In fact when there is an unusual sex ratio, unusual nesting habits may be suspected. In the Crotophaginae the sex ratio is greatly in favor of the males. The question now arises as to whether the breeding habits are the result of an altered sex ratio or the converse. Sarasin (1924) believes that polyandry is the cause of social parasitism in the Cuckoos. As to the actual reasons for the abnormal sex ratio we know nothing positively although many hypotheses have been suggested.

As a manifestation of abnormal breeding habits a consideration of the frequency of feeding the young is of interest. In *Guirra* the young are fed at long intervals, seldom less than one-half hour (Davis, 1940b), but in *C. ani*, although each individual bird comes to the nest only at long intervals, since several birds are carrying in food the young are fed fairly frequently. Compared with other birds, Herrick (1910) found that young American Cuckoos (*Coccyzus*) were fed every 25 minutes and sometimes as often as every four minutes. Passerine birds sometimes are fed at much shorter intervals. Baldwin and Kendeigh (1927) found that a female House Wren (*Troglodytes aedon*) fed the young 18 times in 34 minutes. Bigglestone (1913) found that Yellow Warblers (*Dendroica aestiva*) fed the young over a period of ten days more than 16 times per hour. In the Crotophaginae in addition to the factor of the infrequent feeding is the fact that not all the females incubate even though they may have laid eggs. These facts all indicate a most casual care of the young birds. Neither is the behavior of the adult birds at the nest highly developed. There is no ceremony at the nest at the exchange of incubators or at feeding. The adults do not carry away the egg shells or excreta from the nest. In some

Cuckoos (Herrick, 1910) the adults await the defecation and then remove or eat the fecal sac. No such behavior exists in the Crotophaginae. The excreta are not even contained in a sac.

The analysis of the factors responsible for the construction of abortive nests and the performance of symbolic activities is pertinent to the problem of aberrant breeding habits. It has been shown for *C. ani* that, at the first part of the season, many nests are started and then neglected. The usual explanation of this type of behavior is that the bird's reactions are not yet of sufficient intensity; a statement which explains nothing. Tinbergen (1939) describes these behaviors as "unfinished actions so typical of maturing instinctive behavior." That there can be a lack of adequate stimulus for the completion of a nest is shown by the work of Ali (1930) on a Weaver Finch (*Ploceus philippensis*). He found that the number of females per male in this polygynous species depends on the number of nests the male can build. At the end of the season many cock nests are built by males whose 'zeal' is insufficient to finish the nest. But on the other hand, it must be remembered that in many cases the abortion of a nest may be caused by the lack of a suitable location. Bennett (1938) found that female Blue-winged Teal (*Querquedula discors*) inspected many nesting sites before selecting a suitable location. Abortive nests were frequently started in unsuitable locations—as generally occurs in the duck family.

The question of mutual stimulation among members of the flock must be considered in relation to the egg-laying and the abortion of nests. This hypothesis has been developed by Darling (1938) to explain the behavior of groups of gulls. His evidence indicated that reciprocal stimulation among the members of the flock was conducive to greater success in nesting. In the flocks of Crotophaginae, mutual stimulation may be important in the stimulation of egg-laying and incubation, although the data do not show that large colonies were more successful than small ones. Other species show stimulation by the group. Lack and Emlen (1939) found that all birds in a colony of Tricolor Redwings (*Agelaius tricolor*) are in the same state of breeding. But nearby colonies may differ greatly in their respective stages of breeding. Hoogerwerf (1937) found that the White Ibises, which nest in groups on a platform, were in the same stage of nesting on each platform. Appar-

ently courtship (in the broad sense) can be effective beyond the actual mate.

TYPE OF HABITAT

The importance of the influence of the habitat on the development of social nesting habits is difficult to assess. *Guira* inhabits areas of open park-land savanna and sleeps in clumps of dense trees. Also, the birds tend to nest in thickly foliated trees. Since there are not many groups of such trees the tendency is for the birds to come together in flocks. The original habitat of *Guira* was probably the Chaco and the campos of Brazil. These areas are characterized by open stretches of grass or marsh with scattered clumps of trees. The birds, able to feed out in the open, are thus forced to come together to sleep and nest. Although these islands of trees sometimes are very large, nevertheless there is the tendency for the birds to gather together. It seems likely that the flock habit developed in part under the influence of the habitat. It is of interest that the California Woodpecker, another species with comparable habits, also occurs in areas where the vegetation is distributed in islands. Ritter (1938) states that this woodpecker inhabits forest islands and that the boundaries of the island limit the area of one group of birds.

Crotophaga major and *C. ani* also inhabit more or less open areas, although they return to trees for sleeping and nesting. *Major* is frequently found along the forest edge but never in the thick forest. It lives along the borders of streams, probably because of the nature of the food. Both *Guira* and *C. ani* inhabit mesic habitats. The latter is strictly a moist habitat bird; in Cuba, in the dry season, the birds are found only along the streams, and in Argentina the birds stay throughout the year along streams. The habit of feeding in more open areas and of sleeping and nesting in a clump of trees, presumably developed by the ancestral birds and still to be observed in the primitive *Guira*, has been retained by the genus *Crotophaga*. These considerations suggest the conclusion that the type of habitat in which the species originated and the tendency to divide the territory into a nesting and a feeding habitat have been factors conducive to the development of social nesting.

The habit of sleeping in large flocks occurs in other species, as, for example, *Molothrus* and *Muscivora* as reported by Davis (1940b). In

these species, however, there has been no factor conducive to the breakdown of territorialism and no social behavior has developed. Friedmann (1935) points out that colonial nesting persisted in, or developed in, those species which use separate feeding and nesting ground. When the same ecological habitat is used for both feeding and nesting, colonial nesting does not usually develop. Many species have the territory divided into two distinct parts. A. H. Miller (1931) found that shrikes had a definite headquarters in their territory where the birds slept. Mayr (1926) found that a finch (*Serinus*) used different associations for various purposes such as living, dancing, and feeding. Steinbacher (1939) found that Gallinules (*Gallinula chloropus*) defended a resting place, pairing territory, and a nesting territory. Pettingill (1936) found that the male Woodcock (*Philohela minor*) inhabited the woods in the daytime and the fields at night. These selected examples show that the ecological separation of the territory into several parts is a common occurrence among birds.

PHYLOGENY OF BEHAVIOR

The phylogenetic development of the flock habit is clearly shown by the behavior of the four species of the Crotophaginae. As mentioned in the introduction, *Guira* is the most primitive member of the subfamily both anatomically and behavioristically. *C. major* is the next in the phylogenetic scale. *C. ani* and *C. sulcirostris* resemble one another and represent the climax of development. In *Guira* the flock is a loosely coordinated group of birds, feeding in the same vicinity, sleeping together and, although frequently nesting in pairs, regularly nesting communally. In *Crotophaga major* the flock is more united and always nests communally, although pairs which live singly may nest singly. The flock behavior reached the climax in *C. ani* and *C. sulcirostris*. In these species the group lives together in a closely-knit organization and nests communally. It is of interest to contrast this behavior with that of other flocking species, such as the Oyster Catcher (Huxley, 1925). In this species pairs leave the flock to go to the breeding territory for a while and may collect in flocks until the eggs are laid. But the strict maintenance of territorial boundaries prevents the encroachment by the flock upon the territory of a pair. Hence social nesting is impossible.

The breakdown and redevelopment of the territorial behavior is also a phylogenetic trend. In *Guirra* the defense of the territory by the pair is weak and that by the colony is also weak. In *C. major* the defense of a colonial territory is positive but nevertheless not vigorous. In *C. ani* the defense of the territory by the whole colony is fierce and effective and pair territory has vanished.

This summary of the phylogeny of territorialism in the Crotophaginae suggests the consideration of the relation of this subfamily to the development of parasitism in the other Cuculidae. Herrick (1910) suggests that a maladjustment of the nest-building and egg-laying results in parasitism—a statement which is an outline of the problem but not a solution. Allen (1925) emphasizes the fact that no one theory should be expected to account for the development of the several types of parasitism. He further outlines the distinction between egg-parasitism and nest-parasitism. This scheme has been verified by subsequent research and is followed in this paper. The cuckoos and ducks (egg-parasitism) developed parasitism by dropping eggs occasionally in the nests of other birds, although also building their own nests as, for example, in the Redhead (*Nyroca americana*). On the other hand, the Cowbirds (nest-parasitism) developed parasitism by stealing the nests of other birds or using old nests. The latter trait is common in the Mourning Dove (Nice, 1922) and habitual in the Solitary Sandpiper (*Tringa solitaria*). In these species certain behaviors (regurgitative feeding, precocial habits) precluded the development of parasitism. Davis (1940a) strongly supports these ideas. Friedmann (1928b) accepts this suggestion as a partial solution for Cowbirds. In addition, he emphasizes, there must be a loss of territorialism.

The evidence from the phylogeny of the Crotophaginae indicates that the Cowbirds and the Cuckoos have in common the modification of territorialism but that the other patterns of behavior in the species precluded the identical development of the habit. In the Cuculidae the courtship is weak or absent and the ovulation is spontaneous. Territorialism is retained in a much modified form but the spontaneous ovulation permits the laying of eggs in other birds' nests. From occasional laying in other nests some species developed the habit of always laying parasitically. That the tendency to lay eggs promiscuously occurs

in nonparasitic members of the family is shown by the fact that Pemberton (1925) found the egg of a *Geococcyx* in the nest of a raven; he wrongly interprets this occurrence as deliberate parasitism. In the Cowbirds, in contrast to the Cuckoos, the courtship is retained and elaborated and ovulation is probably non-spontaneous. In these species the usurpation of a nest is necessary when the birds do not build their own nests. From the usurpation of a nest it is an easy step to laying in the nests of other species. These Cowbirds have developed parasitism in a very different manner and even the result, although superficially very similar, is different in many details.

The place of the Crotophaginae in the phylogeny of the parasitic cuckoos is worth consideration. Makatsch (1934) believes that the Crotophaginae represent a stage in the development of parasitism; that after a communal nesting habit, the next stage is true parasitism of other species. The evidence presented in this paper shows that the Crotophaginae represent not a stage in the development but an offshoot. Daguerre (1924) suggests that communal nesting developed as parasitism of one pair on the other. This would assume that there occurred the development of two phases within the species; one parasitic and the other non-parasitic. The fact that in some cases all birds take part in incubation and feeding precludes this interpretation.

The consideration of the phylogeny of behavior and the relation to parasitism in general suggest the desirability of a few inferences as to the future of the group Crotophaginae. At the present time the group seems to be at the climax of possible development. The species are universally successful as is shown by the fact that they are among the most abundant birds in their range. Low temperature seems to be the only barrier to their distribution. Their social habits help the individuals to avoid enemies. Nevertheless one purely hypothetical course of evolution is open to the group. It has been found that the birds are extremely indolent in their attentions to the nest. Individuals which laid eggs did not incubate. Birds which incubated did not feed the young. It is possible that a parasitic phase could develop within the species. Those individuals which lost the instinct of building the nest could survive by laying in the nest built by others. Thus a parasitic phase might develop. If this phase should evolve some morphological characteristic we

should then have the evolution of a new species—perhaps the evolution of two new species. In this connection it should be remembered that many of the parasitic birds (Cowbirds, Viduinae) parasitize closely related species. It is, however, not intended to suggest that all these actually did develop parasitism in exactly this manner.

SUMMARY

The Crotophaginae, one of the six subfamilies of Cuckoos, demonstrates the phylogeny of communal nesting. The birds live in flocks and build one nest in which several females lay eggs. The subfamily consists of four species, distributed throughout South and Central America. The development of social nesting occurs at three levels, represented by the species: I. *Guira guira*, II. *Crotophaga major*, III. *C. ani* and *C. sulcirostris*. The primary factors conducive to the development of social nesting habits are (a) modification of territorialism, (b) aberrant breeding habits, and (c) the type of habitat.

During the investigation the behavior of *Crotophaga ani* was found to be essentially identical in three widely separated localities; Cuba, British Guiana, and Argentina. The call notes of the members of the subfamily are similar as well as other behavior patterns. Some evidence concerning the problems of discrimination of the sex-partner, of the individuals of the species, and of the boundaries of the territory was obtained. The sex-partner and other individuals of the flock are recognized by individual appearance. Strange birds probably are first discriminated by their behavior and then by appearance. The boundaries of the territories are known exactly by the trees and shrubs. Some of the behavior patterns exhibited by the species may be classed as releasers or sign-stimuli. Thus the birds gave the same response to an injury-feigning dove as to an injured member of their own species.

Each flock of all four species maintains a territory. However, the details differ in each case. *Guira* defends the territory only slightly and frequently one pair builds a nest and defends a small territory within the territory of the flock. The flock of *C. major* is composed of pairs which unite to defend a territory. Thus the colony is really a group of pairs which cooperate to build one nest. In *C. ani* the communal nesting has reached its climax. Polygamy or promiscuity is the general rule and the whole colony defends the territory.

This phylogenetic development of social nesting coincides with the disappearance of territorial defense by the pair and the appearance of territorial defense by the colony. Several factors have contributed to the breakdown of territorialism for the pair. Sexual fighting is weak or absent. There is no song in any of the species. Courtship performances are lacking or simple. In these species the biological value of the territory is probably merely the provision of a mating station and nest site. The obvious development, within one group of birds, of a colonial territory from a pair territory, suggests the usefulness of an inclusive, flexible characterization of the term territorialism instead of a strict definition. The behavior of the Crotophaginae further shows that sexual fighting (in reference to the sex-partner) must be clearly separated from territorial fighting (in reference to a piece of land). Territorialism probably originated from the defense of a spot of land on which the sexual bonds can be formed and the eggs laid.

The aberrant breeding habits of the various species permitted the development of social nesting. Several minor factors are of interest. The species have a continuous molt. The sex ratio is in favor of the males. The birds are indolent in the care of the nest, feeding the young at long intervals, and incubating sporadically. Many abortive nests are started and many eggs dropped on the ground or laid in the nest before completion of construction. The important factor is that the Crotophaginae, judging by indirect evidence, ovulate spontaneously and thus do not require courtship performances and pair formation for successful laying. This spontaneous ovulation raises the general problem of internal and external control of a neuro-endocrine mechanism. As one example the data indicate that members of the subfamily lay six eggs normally, therefore the hypophyseal-ovarian mechanism is set to lay a fixed number of eggs no matter how many are in the nest.

The third factor conducive to the development of social nesting habits is the type of habitat. The original habitat was probably a region containing scattered clumps of trees, such as the Chaco or the campos of Brazil. The birds are thus forced to come together to sleep and nest in the trees. This primitive habit is retained in the more evolved species of the subfamily which use different parts of the territory for feeding and nesting.

This subfamily of Cuckoos has developed the social nesting habits, in contrast to the parasitism evolved by the other Cuckoos. Social nesting,

however, is probably not a stage in the development of parasitism but a side branch in the evolution of a peculiar nesting habit.

LIST OF LITERATURE

- ALLEN, G. M. 1925. Birds and Their Attributes. Marshall Jones Co. Pp. 338.
- ALI, S. A. 1930. The nesting habits of the Baya (*Ploceus philippinus*). *J. Bombay Nat. Hist. Soc.*, 34: 947-964.
- BALDWIN, S. P., and KENDEIGH, S. C. 1927. Attentiveness and inattentiveness in the nesting behavior of the House Wren. *Auk*, 44: 206-216.
- BENNETT, LOGAN J. 1938. The Blue-winged Teal. Collegiate Press, Ames, Iowa. Pp. 144.
- BENT, A. C. 1940. Life histories of North American Cuckoos, Goatsuckers, Hummingbirds and their allies. *U. S. Nat. Mus. Bull.* 176. Pp. 506.
- BIGGLESTONE, H. C. 1913. A study of the nesting behavior of the Yellow Warbler (*Dendroica a. aestiva*). *Wilson Bull.*, 25: 48-67.
- BREDER, C. M. 1936. The reproductive habits of the North American Sunfishes (Centrarchidae). *Zoologica*, 21: 1-48.
- BREWSTER, WILLIAM. 1898. Revival of the sexual passion of birds in autumn. *Auk*, 15: 194-195.
- CARPENTER, C. R. 1933. Psychobiological studies of social behavior in aves. *J. Comp. Psychol.*, 16: 25-98.
- CHANCE, EDGAR. 1922. The Cuckoo's Secret. London. Pp. 239.
- CHAPMAN, F. M. 1928. Nesting habits of Wagler's Oropendola (*Zarhynchus wagleri*) on Barro Colorado Island. *Bull. Am. Mus. Nat. Hist.*, 58: 123-166.
- . 1935. The courtship of Gould's Manakin (*Manacus v. vitellinus*) on Barro Colorado Island, Canal Zone. *Bull. Am. Mus. Nat. Hist.*, 68: 471-525.
- CRAIG, WALLACE. 1911. Oviposition induced by the male in pigeons. *J. Morph.*, 22: 299-305.
- . 1913. The stimulation and the inhibition of ovulation in birds and mammals. *J. Anim. Behavior*, 3: 215-221.
- DARLING, F. FRASER. 1938. Bird Flocks and the Breeding Cycle. Cambridge Univ. Press. Pp. 124.
- DAGUERRE, J. B. 1924. Apuntos sobre algunas aves de la Provincia de Buenos Aires. *El Hornero*, 3: 248-252.
- DAVIS, DAVID E. 1940a. Social nesting habits of the Smooth-billed Ani. *Auk*, 57: 179-218.
- . 1940b. Social nesting habits of *Guirra guira*. *Auk*, 57: 472-484.
- . 1940c. A suggestion concerning territorialism in *Tapera naevia*. *Wilson Bull.*, 52: 208.
- . 1941a. Social nesting habits of *Crotophaga major*. *Auk*, 58: 179.
- . 1941b. The belligerency of the Kingbird. *Wilson Bull.*, 53: 157.
- DOMM, L. V. 1939. Modification in sex and secondary sexual characters in birds. In *Sex and Internal Secretions*. Editor, Edgar Allen. Williams and Wilkins Co. Pp. 227-327.
- EMERSON, A. E. 1938. Termite nests—a study of the phylogeny of behavior. *Ecol. Monog.*, 8: 247-284.
- ERRINGTON, P. L. 1933. The nesting and the life equation of the Wisconsin Bob-White. *Wilson Bull.*, 45: 122-132.
- EVANS, L. T. 1936. Territorial behavior of normal and castrated females of *Anolis carolinensis*. *J. Genetic Psychol.*, 49: 49-60.
- . 1937. Differential effects of the ovarian hormones on the territorial reaction time of female *Anolis carolinensis*. *Physiol. Zool.*, 10: 456-463.
- . 1938. Cuban field studies on the territoriality of the lizard *Anolis sagrei*. *J. Comp. Psychol.*, 25: 97-125.
- , and CLAPP, M. L. 1940. The relation of thyroid extract to territorial behavior and to anoxemia in *Anolis carolinensis*. *J. Comp. Psychol.*, 29: 277-283.
- FARLEY, J. A. 1924. Argentine birds. *Auk*, 41: 169-170.
- FAUTIN, REED W. 1940. The establishment and maintenance of territories by the Yellow-headed Blackbird in Utah. *The Great Basin Naturalist*, 1: 75-90.
- FRIEDMANN, H. 1928a. The origin of host specificity in the parasitic habit in the Cuculidae. *Auk*, 45: 33-38.
- . 1928b. Social parasitism in birds. *QUART. REV. BIOL.*, 3: 554-569.
- . 1929. The Cowbirds. C. C Thomas. Pp. 421.
- . 1930. The sociable Weaver Bird of South Africa. *Nat. Hist.*, 30: 205-212.
- . 1932. The parasitic habit in the ducks; a theoretical consideration. *Proc. U. S. Nat. Mus.*, 80(18): 1-7.
- . 1933. The size and measurement of territory in birds. *Bird-Banding*, 4: 41-45.
- . 1935. Bird Societies. In *A Handbook of Social Psychology*. Editor, C. Murchison. Worcester, Mass. Pp. 142-184.

- GOSNELL, H. T. 1932. Two cuckoos laying in the same nest without rivalry. *Brit. Birds*, 26: 226.
- HANN, H. W. 1937. Life history of the Ovenbird in Southern Michigan. *WILSON BULL.*, 49: 146-237.
- HARPER, E. H. 1904. The fertilization and early development of the pigeon's egg. *Am. J. Anat.*, 3: 349-356.
- HERRICK, FRANCIS. 1910. Life and behavior of the Cuckoo. *J. Exp. Zool.*, 9: 169-234.
- HOOGWERK, A. 1937. Uit het leven der witte ibissen (*Threskiornis aethiopicus melanocephalus*) *Limosa*, 10:137-146.
- HUBBS, C. L., AND BAILEY, R. M. 1938. The Small-mouthed Bass. *Cranbrook Inst. Sci. Bull.* No. 10: 1-89.
- HUXLEY, J. S. 1914. The courtship habits of the Great Crested Grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. *Proc. Zool. Soc., London*. Pp. 491-562.
- . 1916. Bird watching and biological science. *Auk*, 33: 142-161, 256-270.
- . 1921. The accessory nature of many structures and habits associated with courtship. *Nature*, 108: 565-566.
- . 1925. Studies on the courtship and sexual life of birds. V. Oyster Catcher (*Haematopus ostralegus* L.). *Ibis*. Pp. 868-897.
- KIRKMAN, F. B. 1937. Bird Behavior. T. Nelson and Sons, London. Pp. 232.
- LACK, DAVID. 1935. Territory and polygamy in a Bishop-bird, *Euplectes h. hordacea* (L.). *Ibis*. Pp. 817-836.
- . 1939a. The behavior of the Robin—life history, territory. *Proc. Zool. Soc., London*. A109. 169-219.
- . 1939b. The display of the Blackcock. *Brit. Birds*, 32: 290-303.
- . 1940. Courtship feeding in birds. *Auk*, 57: 169-178.
- , and EMLIN, J. T. 1939. Observations on breeding behavior in Tricolored Redwings. *Condor*, 41: 225-230.
- , and LACK, L. 1933. Territory reviewed. *Brit. Birds*, 27: 179-199.
- LEACH, FRANK A. 1925. Communism in the California Woodpecker. *Condor*, 27: 12-19.
- LINSDALE, J. M. 1937. Natural history of Magpies. *Pacific Coast Avifauna*, 25: 1-234.
- LORENZ, K. 1931. Beiträge zur Ethologie sozialer Corviden. *J. f. Ornith.*, 79: 67-127.
- . 1935. Der Kumpan in der Umwelt des Vogels. *J. f. Ornith.*, 83: 137-213, 289-413.
- . 1938. A contribution to the comparative sociology of colonial-nesting birds. *Proc. 8th Intern. Ornith. Cong.* Pp. 207-218.
- MAKATSCH, W. 1934. Ueber die phylogenetische Entwicklung des Brutparasitismus. *Beitr. Fort. der Vogel*, 10: 61-65.
- . 1937. Der Brutparasitismus der Kuckucks-vogel. Quelle und Meyer, Leipzig. Pp. 152.
- MAKKINK, G. F. 1936. An attempt at an ethogram of the European Avocet (*Recurvirostra avocella* L.) with ethological and psychological remarks. *Ardea*, 25: 1-62.
- MARSHALL, F. H. A. 1936. Sexual periodicity and the causes which determine it. *Phil. Trans. Roy. Soc., London*, B, 226: 423-456.
- MAYR, E. 1926. Die Ausbreitung des Girlitz (*Serinus canaria serinus* L.). *J. f. Ornith.*, 74: 572-671.
- . 1939. The sex ratio in wild birds. *Am. Nat.*, 73: 156-179.
- MCILHENNY, E. A. 1937. Life history of the Boat-tailed Grackle in Louisiana. *Auk*, 54: 274-295.
- MEISE, W. 1936. Neue Ergebnisse der Revierforschung. *Mitt. Ver. sachs. Ornith.*, 5: 1-23.
- MICHENER, H., and MICHENER, J. R. 1935. Mockingbirds, their territories and individualities. *Condor*, 37: 97-140.
- MILLER, A. H. 1931. Systematic revision and natural history of the American Shrikes (*Lanius*). *Univ. Cal. Pub. Zool.*, 38: 11-242.
- MILLER, L. 1930. The territorial concept in the Horned Owl. *Condor*, 32: 290-291.
- NETHERSOLE-THOMPSON, D. 1934. Some aspects of the territory theory. *Oolog. Record*, 14: 15-23, 79-93.
- NICE, M. M. 1922-23. A study of the nesting of Mourning Doves. *Auk*, 39: 457-474, 40: 37-58.
- . 1933. The theory of territorialism and its development. In *Fifty Years' Progress in American Ornithology*. Pp. 89-100.
- . 1937. Studies in the life history of the Song Sparrow I. *Trans. Linn. Soc., New York*, 4: 1-247.
- NOBLE, G. K. 1936. Courtship and sexual selection of the Flicker. *Auk*, 53: 269-282.
- . 1938. Sexual selection among fishes. *Biol. Rev.*, 13: 133-158.
- . 1940. The experimental animal from the naturalist's point of view. *Am. Nat.*, 73: 113-126.
- , and CURTIS, B. 1939. The social behavior of the Jewel Fish, *Hemichromis bimaculatus* Gill. *Bull. Am. Mus. Nat. Hist.*, 76: 1-46.
- , and VOGT, W. 1935. An experimental study of sex recognition in birds. *Auk*, 52: 278-286.
- , WURM, M., and SCHMIDT, A. 1938. Social behavior of the Black-crowned Night Heron. *Auk*, 55: 7-40.
- ODUM, EUGENE P. 1941. (In litt.)
- PEMBERTON, J. R. 1925. Parasitism in the Roadrunner. *Condor*, 27: 35.
- PETTINGILL, O. S. 1936. The American Woodcock. *Mem. Boston Soc. Nat. Hist.*, 9: 167-391.
- PHILLIPS, C. A. 1887. Egg-laying extraordinary in *Colaptes auratus*. *Auk*, 4: 346.

- RITTER, W. E. 1938. The California Woodpecker and I. Univ. of Cal. Press. Pp. 340.
- RUSSELL, E. S. 1934. The Behavior of Animals. E. Arnold, London. Pp. 184.
- RYVES, B. H. 1929. Three Redshanks at one nest. *Brit. Birds*, 23: 103.
- SALOMONSEN, FINN. 1939. Molts and sequences of plumage in the Rock Ptarmigan (*Lagopus mutus* (Montin)). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*. 103: 1-491.
- SARASIN, PAUL. 1924. Der Brutparasitismus des Kuckucks und die Zahlverhältnis der Geschlechter. Wagner'sche Universitäts-Buchhandlung, Innsbruck. Pp. 6-18.
- DE SCHAUNESSEE, A. 1928. A collection of birds from Siam. *Proc. Acad. Nat. Sci., Phila.*, 80: 571.
- SCHUZ, ERNST. 1936. The White Stork as a subject of research. *Bird-Banding*, 7: 99-107.
- SELOUS, EDMUND. 1933. Evolution of habit in birds. Constable and Co., London. Pp. 296.
- SKUTCH, A. F. 1931. The life history of Rieffer's Hummingbird (*Amazilia t. tzacatl*) in Panama and Honduras. *Auk*, 48: 481-500.
- . 1935. Helpers at the nest. *Auk*, 52: 257-273.
- . 1940. Social and sleeping habits of Central American Wrens. *Auk*, 57: 293-312.
- STEINBACHER, GEORG. 1939. Zur Brutbiologie des Grunfussigen Teichhuhns (*Gallinula chloropus*, L.). *J. f. Ornith.*, 87: 115-135.
- TINBERGEN, N. 1935. The behavior of the Red-backed Phalarope (*Phalaropus lobatus*, L.) in spring. *Ardea*, 24: 1-42.
- . 1939. The behavior of the Snow Bunting in spring. *Trans. Linn. Soc., New York*, 5: 1-94.
- VENABLES, L. S. V., and LACK, D. 1934. Territory in the Great Crested Grebe. *Brit. Birds*, 28: 191-198.
- , and —. 1936. Further notes on territory in the Great Crested Grebe. *Brit. Birds*, 30: 60-69.
- VOGT, WILLIAM. 1938. Preliminary notes on the behavior and ecology of the Eastern Willet. *Proc. Linn. Soc., New York*, 49: 8-42.
- WATSON, J. B. 1908. The behavior of Noddy and Sooty Terns. *Pub. Carnegie Inst.*, 103: 189-255.
- WETMORE, A. 1927. The birds of Puerto Rico and the Virgin Islands. *New York Acad. Sci.*, 9: 245-571.
- WHEELER, W. M. 1923. Social Life Among the Insects. Harcourt, Brace and Co. Pp. 375.
- . 1928. The Social Insects. Harcourt, Brace and Co. Pp. 378.
- WHITMAN, C. O. 1919. The behavior of pigeons. *Carnegie Inst. Washington, Pub.* 257. Pp. 162.
- YAMASHIMA, MARQUIS. 1938. A sociable breeding habit among Timalline birds. *Proc. 9th Intern. Ornith. Cong.* Pp. 453-456.
- YEATES, G. K. 1934. The Life of the Rook. Phillip Allan, London. Pp. 95.





THE INNERVATION OF THE ADRENAL GLAND

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I. THE GROSS ANATOMY OF THE NERVE SUPPLY TO THE ADRENAL GLAND

THE adrenal gland has associated with it a preponderance of nervous tissue which seems far in excess to that which so small a structure might require. This apparent redundancy of nervous tissue can be explained on the basis of two factors. The first of these is most likely related to the ectodermal origin of the medulla. The idea that the adrenal medulla is capable of giving rise to efferent impulses, and thus act as a sort of peripheral nervous center, was proposed by Jacoby (1892), Elliott ('13), Kolmer ('18), and Crile ('31). Rindt and Kahn ('29) could not, however, confirm the findings of the above-mentioned investigators on the neural transmission of adrenalin-invoked impulses. The second of the two factors referred to above is related to the juxtaposition of the adrenal glands to the coeliac plexus. A great portion of the nervous tissue lying in proximity to the adrenals is actually distributed to other organs.

The accepted classification of the autonomic nervous system into sympathetic and parasympathetic divisions will be employed. Though for gross anatomical purposes the splanchnic nerve will be classified as sympathetic, the work of Kure and his many co-workers ('28, '30, '31a, '31b, '31d) on the spinal parasympathetic nerves indicates that this nerve contains parasympathetic as well as sympathetic fibers. Hinsey ('33), in the cat, could not, however, confirm the presence of efferent parasympathetic fibers in the dorsal spinal roots, as maintained by Kure. Nor could Hollinshead ('36) find any degeneration in the splanchnic nerve after sectioning the dorsal roots of the lower thoracic and upper lumbar nerves proximal to their ganglia.

The coeliac plexus (through which the adrenal receives most of its nerve supply) is commonly referred to as sympathetic in nature. In reality it consists of an admixture of parasympathetic (vagus and Kure's spinal parasympathetics) as well as sympathetic elements. Though the vagus

fibers enter the coeliac plexus, they have no functional relationship to the ganglia located therein (Kuntz, 1938). It is because of the sympathetic nature of the coeliac ganglia that the other constituents of this plexus are often erroneously referred to as being entirely sympathetic in nature.

The adrenal plexus is referred to as an offshoot of the coeliac plexus. Superiorly the adrenal plexus is continuous with the inferior phrenic plexus, while inferiorly it joins the renal plexus and also the internal spermatic or ovarian plexus on the left side. These gross anatomical features (Fig. 1) have recently been illustrated in detail by Teitelbaum ('33) on the basis of microscopic dissections in infants. The fibers which make up the adrenal plexus are derived from the splanchnic nerve, the sympathetic trunk, the coeliac ganglion, the vagus nerve, and sometimes the phrenic nerve.

1. The sympathetic nerve supply to the adrenal gland

In contradistinction to its parasympathetic nerve supply, the adrenal gland receives a sympathetic nerve supply, which has its origin in the lower thoracic segments of the spinal cord and traverses the splanchnic nerves and sympathetic trunks to enter the abdomen. The splanchnic nerves make up the more important sympathetic pathway to the adrenal gland. Kure's spinal parasympathetic components of the splanchnic nerve should be kept in mind, however.

The greater splanchnic nerve is generally described as having its origin from about the fifth to the tenth thoracic sympathetic trunk ganglia. Swan (1834), in his detailed anatomical study of the nervous system in man, found the origin of the splanchnic nerve on the right side to be the fifth, seventh, and eighth thoracic trunk ganglia; while on the left side it arose from the fifth to the tenth ganglion inclusive. The lesser splanchnic nerves both arose from the tenth ganglia. Kuntz ('29) states that "the greater splanchnic nerve is formed by the union of several rami arising from the sympathetic trunk between the fifth and ninth or

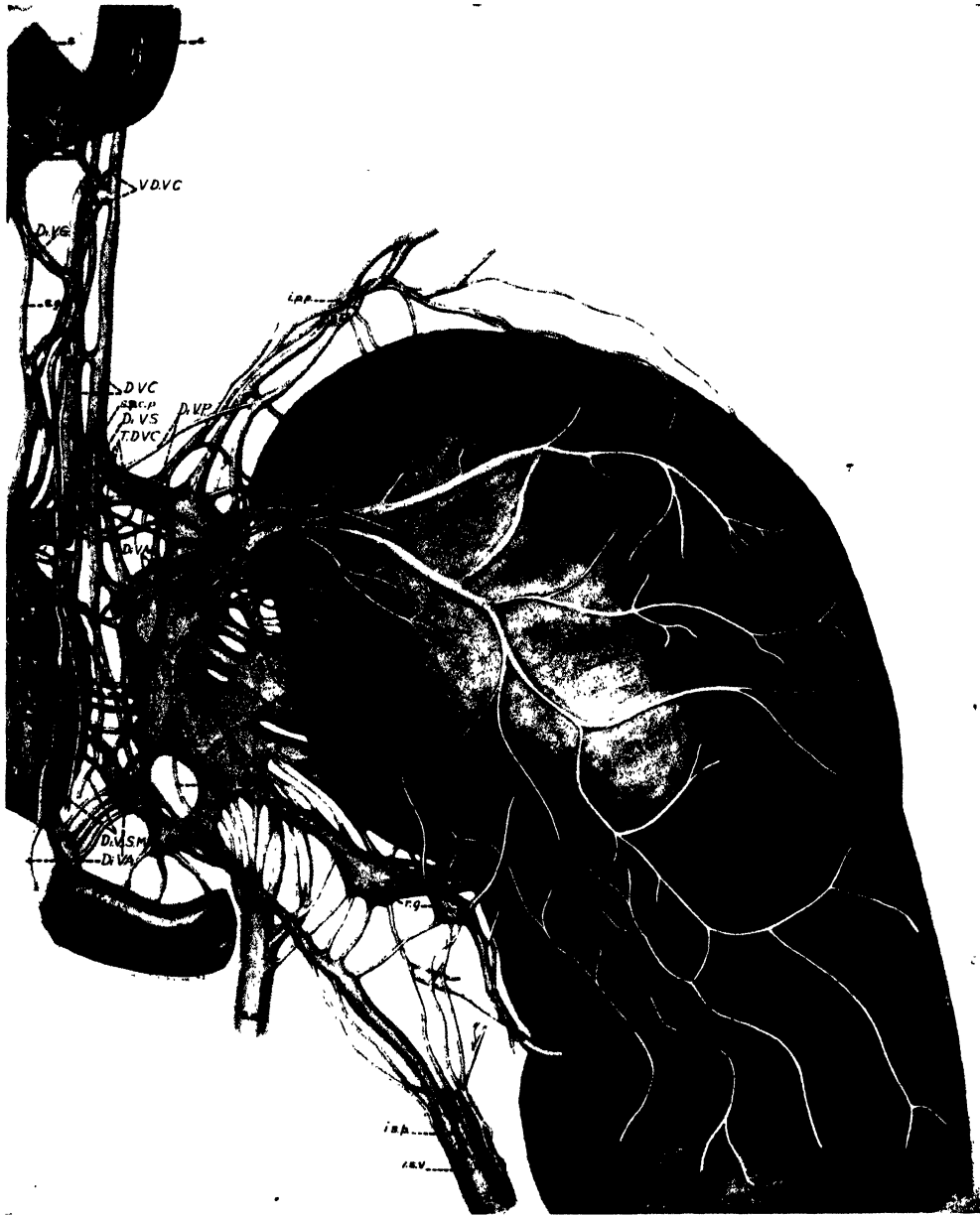


FIG. 1. THE VENTRAL ASPECT OF THE LEFT SUPERIOR QUADRANT OF THE ABDOMINAL CAVITY OF A MALE INFANT

The stomach is rotated to the right on the longitudinal axis of the esophagus, and the tail of the pancreas and splenic vessels have been resected to expose the coeliac plexus and show its relation to the posterior vagus cord and its branches. (The titles of the vagus elements are capitalized.) ad., adrenal gland; cg., coeliac ganglion, left; D.V.C., dorsal vagus cord; Di.V.A., direct vagus rami to aortic plexus; DiV.Ad., direct vagus rami to left adrenal gland; Di.V.G., direct vagus gastric rami; Di.V.I.S., direct vagus ramus to the internal spermatic plexus; Di.V.P., direct vagus ramus to inferior phrenic plexus; Di.V.R., direct vagus ramus to renal plexus; Di.V.S., direct vagus ramus to splenic plexus; Di.V.S.M., direct vagus rami to superior mesenteric plexus; e., esophagus; i.p.p., inferior phrenic plexus; i.s.p., nerves to left internal spermatic plexus; i.s.v., internal spermatic vein; k., left kidney with capsular nerves; p., pancreas (Tail resected); r.g., renal ganglia; r.p., renal plexus; r.v., renal vein; s., stomach; s.a., splenic artery; s.a.n., sympathetic nerves to aortic plexus; s.g., sympathetic gastric nerve; s.p.c.p., splenic plexus contribution to anterior coeliac plexus; T.D.V.C., Terminal branches of dorsal vagus cord; V.D.V.C., Ventral branches of dorsal vagus cord. (From H.A. Teitelbaum., *Anat. Rec.*, v. 55, p. 297, 1933. By courtesy of the Wistar Institute of Anatomy and Biology.)

tenth thoracic ganglia." The lesser splanchnic nerve arises from the ninth and tenth ganglia; while the lowest splanchnic arises from the last thoracic ganglion or from the lesser splanchnic nerve.

Recently Edwards and Baker (1940) studied the variations in the formation of the splanchnic nerves in 100 cadavers. The greater splanchnic nerves were present bilaterally in all instances and varied in origin from the fourth to the twelfth thoracic sympathetic ganglia. The most frequent origin was the seventh, eighth, and ninth ganglia. Only 9 per cent of the cases complied with the typical text book picture. The lesser splanchnic nerve was present on the right side in 93 per cent and on the left in 98 per cent of the cases. They varied in origin from the seventh to the twelfth thoracic sympathetic ganglia but arose most frequently from the tenth and eleventh ganglia. Only 5.5 per cent of the cases complied with the text book picture. The least splanchnic nerve was present on the right side in 89 per cent of the cases and on the left side in 96 per cent. The origin varied from the eleventh and/or twelfth ganglia, the latter being the more common. The text book picture was complied within 82.5 per cent of the cases.

Hollinshead ('36) and Hollinshead and Finkelstein ('37) presented evidence that the adrenal nerves in the cat arise from the lower thoracic and upper lumbar spinal nerves. Swinyard ('37), also in the cat, observed that the last few thoracic spinal nerves give rise to the fibers that supply the adrenal gland. That these nerves are not afferent in nature was demonstrated by Elliott ('13) who excised the dorsal root ganglia of the 5, 6, 7, and 8 thoracic nerves without resulting degeneration of the adrenal fibers. According to Hollinshead, the majority of the adrenal fibers pass to that gland through the lesser splanchnic nerve and the upper lumbar sympathetic chain. Maycock and Hislop ('39) disagree with Hollinshead. The former claim that most of the adrenal secretory fibers traverse the greater and lesser splanchnic nerves. Physiologically, Tournade ('25a, '28) has established the presence of adrenal secretory fibers in the anterior roots of the fourth thoracic to the first lumbar nerves. Young ('38-'39) demonstrated that adrenal fibers leave the cord from segments D6 to L3, with a few fibers from higher and lower fibers in some cases. There was no evidence of contralateral innervation. There is a segmental innervation of the medulla, with the front end

receiving fibers from the more superior roots. Section of the great splanchnic nerve caused degeneration in the anterior half of the medulla.

After piercing the diaphragm, the splanchnic nerves terminate in relation to the coeliac plexus. The greater portion of the efferent fibers in the splanchnic nerves are myelinated, preganglionic fibers which pass to the coeliac ganglion where they have their synapses. The adrenal gland, however, in addition to receiving sympathetic fibers from the coeliac ganglion, also receives direct splanchnic nerves which do not have any synapse in the coeliac or any other intercalated sympathetic ganglion. Noellner (1869), in the dog, and Jacoby (1892), in the dog and rabbit, observed and illustrated branches which passed from the splanchnic nerve directly to the adrenal gland. Biedl (1897) also observed that the splanchnics gave off definite fibers which passed to the adrenal glands without first traversing the coeliac plexus. Biedl names these fibers "Rami suprarenales," and he demonstrated the rôle that they play in the physiology of the adrenal gland. Anatomical verification of Biedl's Rami suprarenales is also offered by Renner ('14, '31) and Hirt ('24). The latter illustrated these fibers in the rabbit and in man.

The credit for actually establishing the directness of the above-mentioned adrenal fibers experimentally apparently goes to Elliott ('13). On sectioning the splanchnic nerve in the cat Elliott found that the myelinated nerves in the adrenal gland degenerated to their terminations in the medulla. Therefore Elliott concluded that the chromaffine cells are innervated directly and not through the intermediation of an intercalated neurone as is usually the case. Elliott's conclusions were confirmed by Hoshi ('27), Hollinshead ('36), and Swinyard ('37).

Golube (1934) showed in the human embryo that the adrenal is innervated by the preganglionic fibers of the great splanchnic nerve during the course of development. These branches go either directly to the adrenal or they traverse the "solaire" ganglia without interruption. Also Golube (1936) demonstrated in the chick embryo that the penetration of the sympathetic cells, which make up the medulla, by the preganglionic sympathetic fibers occurs simultaneously with the development of chromaffine substance.

In his studies on diuretin glycosuria, Nishi ('09) offers some physiological evidence to show that the left splanchnic nerve transmits impulses to the right adrenal gland, but Hoshi ('27) and Young

('38-'39) could not confirm Nishi's observations. After section of the left splanchnic nerve in the rabbit, Hoshi found that while the nerves in the left adrenal medulla degenerated, the nerves in the right adrenal medulla remained quite normal.

In addition to the fibers from the splanchnic nerves and the coeliac ganglion, the adrenal gland also receives a nerve supply from the lumbar sympathetic trunk, according to Elliott ('13), Hollinshead ('36), Young ('38), and Maycock and Hislop ('39). Though the nerves to the adrenal from the coeliac ganglion are not entirely sympathetic in nature, they will be considered as a whole here. When the parasympathetic nerve supply to the adrenal gland is described the vagus constituents of these adrenal nerves will be differentiated from the sympathetic elements.

The various nerves which pass to the adrenal gland go to make up the adrenal plexus. Though the pattern of this plexus is variable in certain details, as in the number of nerves constituting it and in the degree of anastomosis among these nerves, in a general sense its configuration is more or less uniform. This is indicated by a study of the illustrations and descriptions of various anatomists: Walter (1783), Swan (1834), Nagel (1836), Moers (1864), Alexander (1892), Jacobj (1892), Renner ('14, '31), Schkawera and Kusnetzow ('23), Hirt ('24), and Teitelbaum ('33). There is most agreement on the relationship between the adrenal plexus and the renal and inferior phrenic plexuses, as well as on the contributions from the splanchnic nerves. There is extreme variation in the depiction of a capsular adrenal plexus. Swan (1834) fails to show such a plexus in man, while Teitelbaum ('33) illustrates a rather extensive one (Fig. 1) with relatively few anastomoses in the human infant. Many nerves pierce the adrenal parenchyma directly. Undoubtedly the capsular plexus may be either present or absent.

Hirt ('24) observed contributions to the right adrenal gland from an "epiphrenic" ganglion in man. This epiphrenic ganglion, which receives fibers from the coeliac ganglion and which contributes fibers to the diaphragm in addition to the adrenal, is most likely an aberrantly located piece of the coeliac ganglion. Small microscopic ganglia have been observed in the fibers of the adrenal plexus by many of the above-mentioned investigators. Also, according to Moers (1864) and Alexander (1892), the phrenic nerve contributes fibers to the adrenal plexus.

B. The parasympathetic nerve supply to the adrenal gland

Before describing the actual distribution of the vagus fibers to the adrenal gland, it is important to consider certain pertinent facts with relation to the thoracic course of the vagi. From the descriptions offered in certain anatomy texts, as recently pointed out by Teitelbaum ('33), and as is evident in Laterjet and Rochet ('23), Braus ('24), Robinson ('25, '31), Laterjet (30), Huber (30), and still others not mentioned here, one gets the impression that each vagus nerve passes through the thorax and reaches the abdomen as a distinct entity. It is a generally accepted anatomical fact that inferior to the pulmonary roots, the two vagi take up certain positions in relation to the anterior and posterior walls of the esophagus. According to the above-mentioned texts, the right vagus enters the abdomen on the posterior aspect of the esophagus, and the left vagus on the anterior aspect of the esophagus. Though the above is in compliance with embryological data, Arey ('30), there is sufficient anatomical evidence to indicate that the vagus nerves at the level of the diaphragm can no longer be correctly considered as right and left respectively in the same sense that they are so called in their course superior to the roots of the lungs. On the basis of dissections and degeneration experiments, it has been definitely established by Swan (1834), Kollman (1860), Jacobj (1892), Wertheimer ('01), Iwama ('25), McCrea ('25), Brauecker ('27), Uchida ('28), Teitelbaum and Uhlenhuth ('32), and Teitelbaum ('33) that caudal to the roots of the lungs each vagus nerve contributes fibers to both the anterior and posterior surfaces of the esophagus to make up the anterior and posterior esophageal plexuses respectively. At the inferior ends of these plexuses, the vagus fibers converge to form two trunks or cords, the anterior and posterior vagus cords (Fig. 2), each lying on its respective surface of the esophagus. Each of these cords, because of the anastomoses which occur in the esophageal plexuses, contains fibers derived from both the right as well as from the left vagus nerve. In experiments carried out in cats, Teitelbaum (unpublished) has been able to verify the findings of Iwama ('25) with relation to the presence of Marchi bodies in both the anterior and the posterior vagus cords after section of either the right or left vagus nerve in the neck.

Though it has been pointed out above that a

number of contemporary texts of anatomy do not describe the distribution of the vagi accurately, as well as anatomical importance is the fact that Vesalius (1725) fails to depict the intervagus

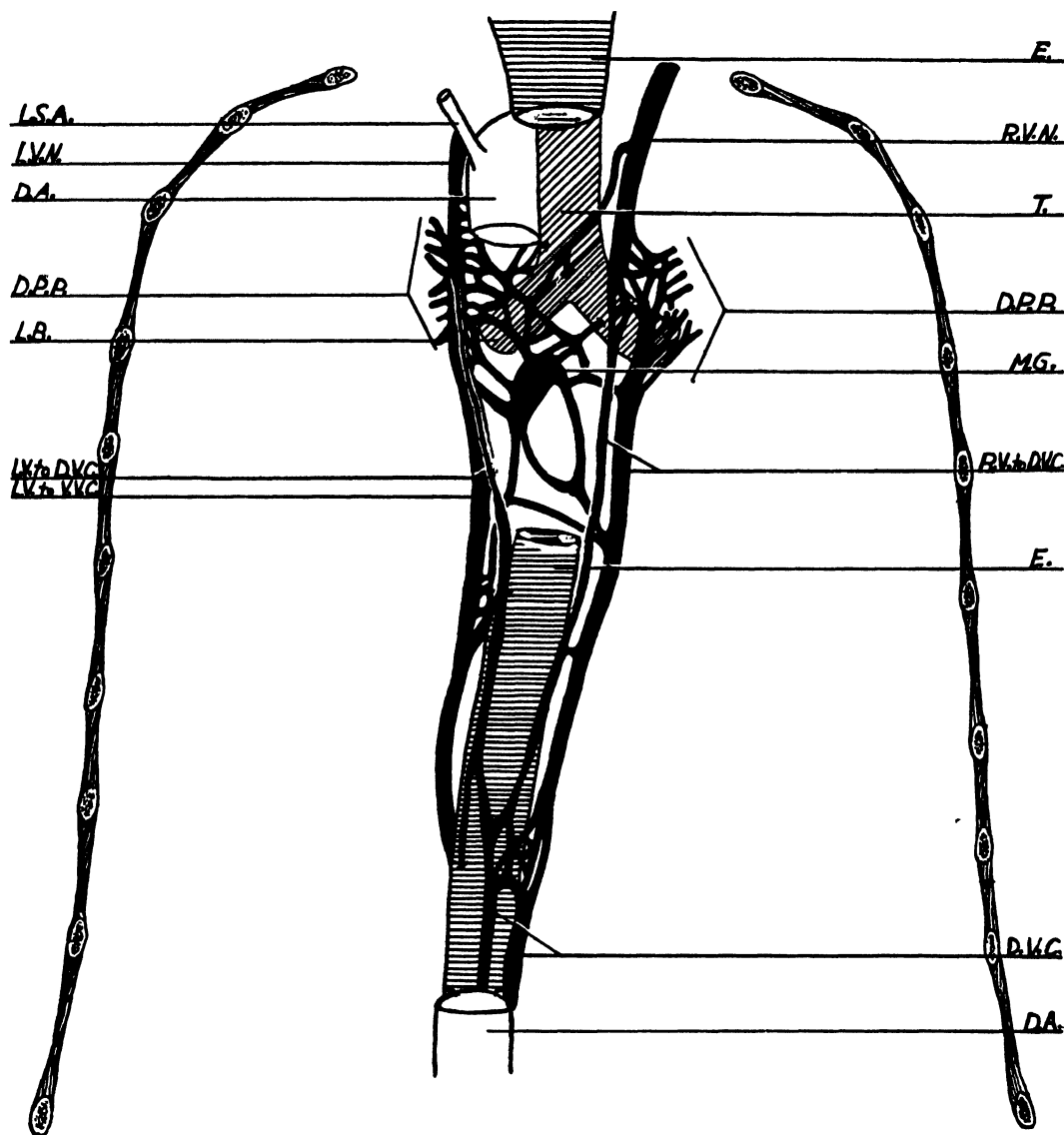


FIG. 2. THE DORSAL VAGUS CORD OF A NEW BORN INFANT DISPLAYED IN A DORSAL DISSECTION

The dorsal thoracic wall has been removed, exposing the dorsal aspects of the thoracic viscera. The dorsal vagus cord is formed by the union of rami derived from the left and right vagus nerves. D.A., descending aorta (partly resected); D.P.P., dorsal pulmonary plexus; D.V.C., dorsal vagus cord; E., esophagus (partly resected); L.B., left bronchus; L.S.A., left subclavian artery; L.V. to D.V.C., left vagus ramus to dorsal vagus cord; L.V.N., left vagus nerve; L.V. to V.V.C., left vagus ramus to ventral vagus cord; M.G., mediastinal ganglion; R.V. to D.V.C., right vagus rami to dorsal vagus cord; R.V.N., right vagus nerve; T., trachea.

(Modified slightly from H A. Teitelbaum and E. Uhlenhuth. *Anat. Rec.*, v. 52, p. 24, 1932. By courtesy of the Wistar Institute of Anatomy and Biology.)

there are a number which do offer accurate descriptions: Jackson ('25), Hovelacque ('27), Robinson ('31), Greving ('31), and others. Of historical

anastomoses in his illustrations; while Willis (1720) and Walter (1783) offer illustrations which demonstrate the distribution of the vagi correctly.

Haller (1766) also describes the intervagus anastomoses about the esophagus.

With the above as a basis, it becomes quite evident that the greater portion of the abdominal viscera, which are erroneously believed by some to receive their parasympathetic nerve supply from the right vagus nerve alone, really are supplied by the posterior vagus cord (Fig. 1), which consists of fibers derived from both the right and left vagus nerves. Evidence to support the bilateral vagus innervation of each adrenal gland is offered by Teitelbaum ('34) on the basis of experiments carried out in the cat by means of the Marchi technique. It is planned to repeat these experiments by means of a more dependable technique. This is particularly important in the light of the negative reports of Hoshi ('27) and Hollinshead ('36).

In addition to the vagus fibers that can be dissected out directly to the adrenal, the latter most likely also receives vagus fibers which pass through the coeliac ganglion, for the greater portion of the posterior vagus cord enters that ganglion (Fig. 1). Teitelbaum ('33) refers to the branches of the posterior vagus cord which pass directly to the abdominal viscera as "direct" branches; while those which pass through the coeliac ganglion before they reach the viscera are named "indirect" vagus branches (Fig. 1). Direct fibers from the posterior vagus cord to the left adrenal gland (Fig. 1, Di.V.Ad.) are described by Kollman (1860), Moers (1864), Alexander (1892), Renner ('14) ('31), McCrea ('25), and Teitelbaum ('33). None of the above mentioned investigators has been able to trace fibers from the posterior vagus cord to the right adrenal, though several of them do express the opinion that the latter organ must receive its vagus nerve supply through the coeliac ganglia. Besides the above, Uchida ('28) describes and illustrates a direct and rather constant contribution from the anterior vagus cord to the left adrenal gland. That the "direct" vagus fibers to the adrenal are not found constantly is illustrated by Teitelbaum ('33).

In contrast to the anatomical findings described above, Hoshi ('27) and Hollinshead ('36) could not demonstrate any changes in the nerve fibers present in the adrenal gland after having sectioned the vagus. Splanchnic section, however, resulted in the degeneration and disappearance of the nerves in the adrenal medulla. In agreement with the above, Kure, Wada and Okinaka ('31c) report that section of both vagi below the diaphragm failed to cause degeneration of the fine medullated fibers

passing to the adrenals. They claim that the vagus has no relation to the adrenal gland, for the parasympathetic nerve supply to the latter is derived from the spinal parasympathetic fibers in the splanchnic nerve. Maycock and Hislop ('39) failed to produce adrenalin secretion by stimulating the vagus.

II. HISTOLOGY OF THE ADRENAL NERVES

Because of the ectodermal origin of the adrenal medulla, and the richness of the adrenal nerve supply, the histological study of the adrenal nerves has been, and still is, a matter of special interest. Among the earlier investigators, Gottschau (1882) thought that the medulla was mostly nervous in nature; while Fusari (1891) sought to establish the sympathicogenetic nature of the adrenal medulla by extensive studies of the intrinsic nerves of that organ. Some of the earlier reports, as well as some of the more recent ones, deny the presence of nerves in the adrenal cortex. There is almost complete agreement, however, on the richness of the nerve supply to the medulla, differences existing only in certain details. Though most reports contain accounts of intrinsic adrenal ganglia and nerve cells, there is no complete accord on this phase of the study. Undoubtedly the presence of ganglia is a matter that varies not only with the species but also with the individual animal, as will be pointed out subsequently.

A. The capsular nerves of the adrenal gland

In the preceding review of the gross anatomy of the adrenal nerves, the inconstant nature of a capsular plexus has already been referred to. Small ganglionic masses in the adrenal nerves have also been mentioned. Histologically, capsular nerves are reported by a number of investigators. Moers (1864) described capsular nerves which contained ganglia, the true nature of which he verified microscopically. Fusari (1891), who made studies in man, mice, rats, rabbits, hogs, cats and goats, observed a capsular plexus which also contained small ganglia. According to him, ganglia are found in, as well as immediately beneath, the capsule. Not all of the nerves that enter the capsule are distributed to the adrenal gland, however, for some of them leave the capsule, and others penetrate the cortex only to alter their course and pass out again. Kolmer ('18) and Hollinshead ('36) have confirmed this observation. Most of the capsular nerves are, however, ultimately distributed to the adrenal parenchyma. Dogiel (1894) also described cap-

sular plexuses in several different species of animals, and he observed that these plexuses were intimately associated with the nerves distributed to the zona glomerulosa and reticularis. In addition to the above, Renner ('14), Kolossow ('30) in the turtle, Alpert ('31) in man, and Pines and Narowtschatowa ('31) in six species of mammals also describe capsular nerves. Renner and Alpert confirm the intimate relationship between the capsular plexus and the nerves in the outer layers of the cortex; while Kolossow, Alpert, Pines and Narowtschatowa, and Hollinshead ('36) confirm the presence of ganglia in the capsule of the adrenal gland.

In histological studies of adult cat and kitten adrenals, Teitelbaum (unpublished) has observed that ganglia of variable size, some quite large, constantly lie in relation to the adrenal gland (Fig. 3). Less frequently some of these ganglia may be buried in the capsule of this gland. Because of the close relationship of the coeliac ganglia to the adrenal glands, especially on the left side, the author is of the opinion that the capsular ganglia of the adrenal gland are really displaced portions of the coeliac ganglion, as in the case of Hirt's "epiphrenic" ganglion, and the renal, or oft-called "aortico-renal," ganglion. Not only do the nerve cells in the adrenal capsular ganglia closely resemble those in the coeliac ganglion of the cat, but in serial sections through a block of abdominal tissue containing the adrenals, coeliac ganglion, and adjacent structure, the continuity of the adrenal capsular ganglia and the coeliac ganglion can often be established.

B. The nerves of the adrenal cortex

1. The parenchymal nerves of the adrenal cortex

Though Nagel (1836) observed that nerves were distributed to the adrenal cortex as well as to the medulla, Moers (1864) claimed that the nerves pass through the cortex to the medulla without being distributed to the cells of the former at all. According to Fusari (1891), Nagel was the only one of the earlier investigators to describe nerves in the adrenal cortex. Fusari also observed many nerves in the cortex. Each capillary, according to him, is accompanied by at least one fine nerve fiber. There are also other nerves which are independent of the blood vessels. The nerve fibers of the adrenal cortex arise either from the capsule or from the medulla; or more rarely from the nerve bundles which pass through the cortex. Concern-

ing the ultimate terminations of the cortical nerves, Fusari states that the cortical cells do not have any intimate relationship with the nerve fibers as is the case in the medulla.

Following Fusari, Dogiel (1894), who studied the adrenal nerves in several species of mammals, classified these nerves into three groups; capsular, cortical, and medullary. Dogiel describes nerve plexuses around the blood vessels of the adrenal gland. The nerves of the capsular plexus are intimately associated with those of the zona glomerulosa, and from the glomerular zone the fibers pass to the zona fasciculata. The fibers which pass between the cell columns of the zona fasciculata anastomose with the fibers of the zona reticularis, which has the richest nerve supply of the three zones in the cortex. The finer branches of the cortical nerves surround the cells in groups. No intercellular nerve endings are present.

Elliott ('13) pointed out that the nerves that pass through the cortex to the medulla are myelinated; and that these nerves degenerate after the splanchnic nerve is sectioned. Renner ('14, '31) confirms most of Dogiel's findings; while Kolmer ('18) observed that nerve trunks pierce the cortex to supply the zona reticularis and the medulla. Some of the nerves pass out again through the cortex, however, to end somewhere else in the sphere of the autonomic nervous system, according to the latter author.

Hoshi ('27), reverting to the earlier conception concerning the absence of nerves in the cortex, denies the fine distribution of nerves among the cortical cell groups. In birds the nerves are distributed only to the medullary cells, according to Hoshi. In mammals the nerves pierce the capsule and cortex to be distributed among the cells in the medulla. Contrary to Hoshi's observations in birds and mammals, Hirt ('30) reports that in frogs (*Rana temporaria* and *R. esculenta*) the fine branches from the plexus on the surface of the adrenal penetrate into the latter, and spread out among the individual cells. Though Hirt could find no nerve endings, he did note that there was no difference in the relationship of the nerves to the medullary and cortical cells.

In the turtle (*Emys europaea*) Kolossow ('30) observed that the cortical (interrenal) tissue of the adrenal is not as richly supplied by nerves as is the medullary tissue. The cortical fibers are thicker than those of the chromaffine tissue, and they surround cell groups rather than individual

cells. Kolossow is of the opinion that the failure to follow the cortical fibers into the cell groups, and see their ultimate termination among the cells, is due to technical difficulties which arise from the presence of the cortical lipoid.

On the basis of the findings already mentioned one might readily conclude that the absence of nerve endings in relation to the individual cortical cells is an established fact, but more recently Alpert ('31), in his detailed study of the human adrenal, came to conclusions diametrically opposed to that mentioned above. 'According to Alpert, the nerves of the cortex are non-myelinated, and they enter either along with the blood vessels or alone. The zona glomerulosa receives its nerve supply from the capsular nerves, and not only the glomerular cell groups, but also the individual cells of these groups are surrounded by nervous networks. In addition, Alpert describes intracellular nerve terminations. The zona fasciculata is supplied by fibers derived both from the capsule as well as from the zona glomerulosa. They pass between the cell columns to which they give off branches. These branches form plexuses around the cell columns, and give rise to fine intercellular as well as intracellular nerve endings. The zona reticularis nerve plexuses which are derived from the fascicular and capsular nerves are richer than those located in the more superficial cortical layers, and they also give rise to pericellular networks and intracellular nerve endings.

Alpert stands more or less alone in his findings concerning the finer details of the nerve endings in the cortex, for even Pines and Narowtschatowa ('31), who studied the adrenal nerve supply in the ox, rabbit, cat, dog, mouse and rat, using the Cajal, Weigert and Nissle techniques, conclude that the cortex is sparsely innervated in comparison to the medulla, and that the nerves end in relation to cell groups rather than individual cells. More recently Hollinshead ('36) in the cat and Swinyard ('37) in the cat and in man, contrary to Alpert, failed to find any definite evidence of cortical innervation.

The extreme differences reported above might be explained either on the basis of the different species of animals studied, or on the basis of technical difficulties involved in staining the nerves in the adrenal cortex, as mentioned by Kolossow. These difficulties have been duly impressed upon the mind of the author in his efforts to stain the adrenal nerves by means of Bielchowsky's pyridine-silver technique. In the case of the cortex, one

must not only contend with connective tissue affinity for the silver, but also with the avidity of the cortical cells themselves for that metal.

2. The vaso-motor nerves of the adrenal cortex

Detailed studies of the terminations of the adrenal nerves in relation to the blood vessels of that gland, as have been made in the thyroid gland, for instance, by Anderson (1894), Briau (1897-98), Rhinehart ('12), Popow ('28), and Nonidez ('31, '32), have not been made—at least not as far as the knowledge of the author is concerned. Fusari (1891) observed that each capillary is accompanied by at least one fine nerve fiber; while Dogiel (1894) states that the nerves form plexuses around the larger blood vessels and capillaries, thus disagreeing somewhat with Fusari, who does not report any plexuses. Alpert ('31) remarks that the nerves may enter the cortex either in company with blood vessels or alone, and that nerves in the zona fasciculata pass between the cell columns along with the blood vessels. In the medulla Alpert found that nerve cells are occasionally located in the walls of the blood vessels. Pine and Narowtschatowa ('31) are no more enlightening on this subject than are their predecessors, for they merely mention the fact that the nerves usually follow the blood vessels. The more recent work of Hollinshead ('36) in the cat reveals that small groups of lone fibers accompany blood vessels into the cortex and lose themselves on the walls of these vessels. In the medulla some fibers run in contact with blood vessels. Nerve fibers can be seen in the media of the vessels, and are apparently concerned with the innervation of the musculature.

Though no detailed histological studies of the terminations of the vaso-motor nerves in the adrenal gland are available, that such nerves actually exist has been well substantiated by many physiological experiments: Biedl (1897), Dreyer (1898-99), Hallion ('21), Schklawera and Kusnetzow ('23) and Kure, Wada and Okinaka ('31c).

3. The intrinsic ganglia of the adrenal cortex

Though there is rather unanimous agreement concerning the existence of capsular ganglia, no such harmony exists with regard to ganglia in the adrenal gland itself. Dogiel (1894) states that nerve cells are present either singly, in small groups, or in ganglia. They are usually located in the nerve trunks, mostly in the medulla, and only rarely in the cortex. That the presence of ganglia

in the adrenal gland varies with the different species, and most likely even with the individuals of any one species, is made quite evident by Dogiel, for he states that nerve cells are most commonly found in the guinea pig, while they are less numerous in the dog and cat, and rare in the rat. Though having studied literally hundreds of sections through cat adrenals, the author has never observed any nerve cells in either the cortex or medulla of that gland. Renner ('14, '31) could find no ganglia in the adrenal cortex; while Hoshi ('27), who seldom observed nerve cells in the cat and guinea pig, failed to find them in the rabbit, either in the cortex or medulla. Though Alpert ('31) and Hollinshead ('36) mention no cortical ganglia, Pines and Narowtschatowa ('31) describe nerve cells in all parts of the adrenal gland, including the cortex. The nerve cells in the adrenal vary considerably in number in different animals according to these authors. They may be multi- or bipolar, and are characteristically sympathetic in nature.

The inconstancy of nerve cells in the adrenal gland is most likely characteristic of the other endocrine glands also. Evidence that such is the case for the thyroid is presented in a recent review on the innervation of that gland by Teitelbaum ('34a).

C. The nerves of the adrenal medulla

1. The parenchymal nerves of the adrenal medulla

In contrast with the negative findings of Hoshi ('27), Hollinshead ('36), and Swinyard ('37) concerning the existence of nerves in the adrenal cortex, there never has been any doubt as to the presence of nerves in the adrenal medulla. As a matter of fact some of the earlier histologists were actually of the opinion that the cells of the adrenal medulla were neural in nature. Moers (1864) refers to the fact that Kolliker believed that the adrenal medulla was made of nerve cells. Moers himself was skeptical of this opinion, but nevertheless he states that if the medullary cells are nervous in nature they are associated with the nerve trunks in the adrenal and not with the adrenal gland itself. Concerning the distribution of the nerves in the medulla, Moers states that after piercing the cortex they branch considerably among the medullary cells. Nagel (1836), who preceded Moers, also observed the branching of the nerves distributed to the adrenal medulla.

Gottschau (1882) believed that the medulla was mostly nervous in nature, but he nevertheless denied that it could really be considered as part of the nervous system. Gottschau came to the conclusion that the medulla fundamentally resembles the cortex; thus, knowingly or unknowingly, he classified it as a glandular organ.

Though these earlier investigators reported the presence of nerves in the adrenal medulla, Fusari (1891) was among the first to give accurate detailed descriptions of the distribution of these nerves. The anastomoses and points of crossing among the small nerve bundles are so numerous, according to Fusari, that the entire medulla contains an extensive plexus of nerve fibers in good preparations. Each group of medullary cells was found to be contained in a reticulum of nerve fibers, the nodes of which were applied to the cells, for the fibers lying in relation to the medullary cells were provided with discoidal nodules or small polygonal plaques.

According to Dogiel (1894), the medulla receives those nerves which are not distributed to the capsule, but which pierce directly into the adrenal parenchyma. The medullary nerves give rise to fine branches which build intricate plexuses among the cells. Varicose fibers penetrate between the cells where they anastomose to form plexuses. Renner ('14, '31) confirms the descriptions presented above, but Kolmer ('18), who found the nerves in the guinea pig medulla to be almost exclusively non-myelinated, could not find any fibers which ended as secretory nerves usually do in glands. Kolmer believed that many of the nerves in the adrenal medulla had their origin in that organ, and he therefore suggested that the nerves arising in the adrenal medulla had different chemical and morphological affinities from those which entered from without. As has been previously mentioned, Kolmer conjectured that the secretory product of the adrenal medulla is in some way released through the adrenal nerves. In the human adrenal Kolmer observed that some myelinated nerves pass to the medulla where they end in lamellated enlargements of complicated pattern. These enlargements have connective tissue sheaths.

In the frog, Hirt ('30) observed that the nerves pass from the adrenal capsule into the parenchyma of that gland, and spread out to surround the individual cells without giving rise to any nerve endings. In the turtle Kolossow ('30) describes

the fine nerves of the chromaffine tissue as penetrating among the strands of medullary cells to form intricate plexuses. The fibers ultimately terminate in relation to the individual cells. One fiber may come in contact with several cells. Contrary to Hirt's observations in the frog, Kolosow reports that the nerve fibers in the turtle medulla bear enlargements which are approximated to the cells. A fine network is discernable in these enlargements. Kolosow is of the opinion that the turtle medulla is not as richly supplied with nerves as is the mammalian adrenal medulla.

Alpert ('31) does not agree with the contention of Dogiel that the nerves to the medulla do not arise from the capsular nerves, but rather from those which pierce the adrenal parenchyma directly. Alpert classifies the nerves to the human adrenal medulla into three groups: (1) Myelinated nerves which arise from the capsule and pass to the medulla where they form synapses with the nerve cells present. These nerves lose their myelin in the medulla. (2) Non-myelinated fibers that are distributed to the region between the zona reticularis and medulla. These pass at right angles to the fibers of group (1), and give rise to branches that pass into the medulla. (3) Nerves in the walls of the large blood vessels that enter the medulla. These are fine and non-myelinated. Concerning the finer ramifications of the medullary nerves, Alpert states that they anastomose little, are finer than the cortical fibers, a condition observed in the turtle by Kolosow, and they enmesh the cells both in groups as well as individually, giving rise to intracellular terminations that end near the nuclei of the chromaffine cells.

Pines and Narowtschatowa ('31) do not agree with Alpert's finer details, for they describe intricate plexuses which give rise to fibers bearing varicosities and intercellular endings. Though no intracellular endings were observed, these authors describe fibrillar end-knobs which end in the connective tissue, and which they consider as afferent in nature. Popow ('28) has described similar endings in the thyroid and he interprets them as afferent also. It must be kept in mind, that while Alpert studied the human adrenal, Pines and Narowtschatowa studied the adrenals of several mammals, not including that of man, however.

More recently Hollinshead ('36) described a delicate plexus in the cat medulla. This surrounded the cell groups, and gave rise to fine fibrils that passed between the cells. The nerve endings consisted of end bulbs and ring-like terminations.

The larger bulbs sometimes resembled cells. No intracellular endings were found. While the smaller fibers were found to cross frequently there was no evidence of anastomosis. Swinyard ('37) confirmed the findings of Hollinshead.

As has already been mentioned, on the basis of the findings of Elliott ('13), Hoshi ('27), Hollinshead ('36), and Swinyard ('37), a good portion of the nerves in the adrenal medulla are preganglionic and splanchnic in origin, and they are supposed to terminate in relation to the cells of the adrenal medulla without the intermediation of an intercalated neuron.

2. The vaso-motor nerves of the adrenal medulla

As in the case of the cortex, few of the investigators mentioned above have paid much attention to the relation of the nerves in the adrenal medulla to the blood vessels of that organ. Alpert ('31) describes ganglion cells as lying in the walls of blood vessels occasionally. According to Pines and Narowtschatowa ('31), nerves follow the blood vessels and branch simultaneously with the latter. Even the smaller vessels are accompanied by nerves. The plexuses, which form about the vessels, give rise to nerve endings which penetrate to the adventitia and media and serve vaso-motor functions. These findings are confirmed by Hollinshead ('36), who was also able to find nerve fibers in the media of the vessels.

3. The intrinsic ganglia of the adrenal medulla

Moers (1864) mentions the presence of ganglia in the adrenal gland. Gottschau (1862), who studied the adrenals of man, cattle, and sheep, observed that there was a preponderance of nerves and nerve cells in the inferior pole of the adrenal. Gottschau was of the opinion that the adrenal medulla was mostly nervous in nature. This conception is most likely the foundation of the theory of neural transmission of adrenalin invoked impulses, as suggested by Jacoby (1892), Elliott ('13), Kolmer ('18), Rindt and Kahn ('29), and Crile ('31). That the chromaffine cells do have a peculiar relation to the nerves in the medulla is evident from the work of Elliott ('13) and Hoshi ('27). Contrary to the condition existing in other organs, the chromaffine cells are innervated by preganglionic rather than postganglionic neurones. This would indicate that these cells are probably modified post-ganglionic neurones.

The finer details of the nerve cells found in the adrenal have been described by Fusari (1891).

According to him, both the large nerve bundles as well as the smaller branches contain nerve cells. The number of these cells varies in different species of animals, being frequent in the rabbit and less numerous in the goat and mouse. The cells measure from 8 to 30 microns in diameter, and are fusiform or spherical in shape. Both types of cells have two prolongations as a rule. In some cases there may be only one process, probably due to the failure of the smaller process to take up the stain; for when two prolongations are present, one is large, and one small. The larger prolongation is continuous with the fibers of the nerve proper, while the smaller one penetrates into the medullary parenchyma in true postganglionic fashion.

Nerve cells may also be found along the sides of nerve bundles, especially in rabbits. These cells are usually spherical and they possess two prolongations, the larger of which joins the bundle while the smaller is distributed to the parenchyma. Other polygonal nerve cells are present and are provided with branched prolongations. These cells are located along the smaller nerve bundles and isolated fibers which are found among the groups of medullary cells.

Dogiel (1894) does not entirely agree with Fusari's description of the nerve cells in the adrenal medulla. He claims that they are most numerous in the guinea pig, less numerous in the dog and cat, and seldom present in the rat. Dogiel describes small and large multipolar cells. The processes of the small cells form plexuses around the larger ones. One of the processes could be followed to the cells of the medulla, as described by Fusari. The significance of the pericellular network in relation to the larger nerve cells is really difficult to surmise. Dogiel claims that bipolar nerve cells may also be present near the multipolar cells.

Though not agreeing with all of the findings of either Fusari (1891) or Dogiel (1894), Renner ('14, '31) confirms some of the observations of both. According to Renner, the medullary nerve cells lie either individually among the chromaffine cells or in groups of 2 to 30. They are of the sympathetic type. The isolated cells have no capsules, but the grouped cells are definitely encapsulated. The processes of the isolated cells end in direct relation to the medullary cells, contrary to Dogiel's observations. The small bipolar cells of Dogiel were found by Renner in several animals, but not in man.

Opposed to Dogiel's (1894) observations in the

guinea pig is the failure of Kolmer ('18) to find any nerve cells in the adrenal medulla of that animal. Though Kolmer believes that nerve cells can be found in some animal forms, he contends that the presence of an abundance of nerve cells in the adrenal medulla, as maintained by the earlier investigators, must be viewed with skepticism. Nerve cells in the adrenal medulla are the exception rather than the rule, according to Kolmer, and his contention is supported by Hoshi ('27) who could not find any nerve cells in either the cortex or medulla of the rabbit. The author's



FIG. 3. GANGLION IN CAPSULE OF ADRENAL GLAND OF THE CAT

The cells of the zona glomerulosa of the cortex are evident with their lipoids stained black. (Marchi technique.)

observations in the cat also confirm Kolmer's views. Hollinshead ('36) could find only few nerve cells in the cat medulla, and these inconsistently.

Alpert ('31) in man, and Pines and Narowtschatowa ('31) in several species of mammals, do not agree with Kolmer. Alpert describes ganglion cells as being present in all parts of the medulla, even in the walls of the blood vessels. Nerve fibers enter the nerve cells and emerge through the processes to terminate among the medullary cells. According to Pines and Narowtschatowa, the nerve cells which are present in all parts of the adrenal, as well as in the nerve bundles themselves, are characteristically sympathetic. They vary

considerably in number, may be isolated or grouped, and either multi- or bipolar.

The significance of the data on the presence or absence of nerve cells in the adrenal medulla is not a matter of mere morphological interest if the findings of Elliott ('13), Hoshi ('27), Hollinshead ('36), and Swinyard ('37) are recalled. If the adrenal medulla does contain a rich supply of nerve cells, then it is possible that the splanchnic nerve preganglionic fibers to the adrenal do not end in direct relation to the chromaffine cells but rather in relation to the nerve cells in the medulla. However, if those are correct who contend that the presence of nerve cells in the adrenal medulla is an exception rather than the rule, then the preganglionic splanchnic fibers do end in direct relation to the chromaffine cells, as maintained by Elliott and Hoshi.

III. SUMMARY

The apparently excessive nerve supply to the adrenal gland is related to its ectodermal organ and to its proximity to the coeliac plexus. The adrenal gland is innervated through the adrenal plexus, which receives its fibers from the splanchnic nerve, sympathetic trunk, coeliac ganglion, vagus nerve, and sometimes the phrenic nerve.

The sympathetic nerves to the adrenal arise in

the lower thoracic spinal segments and traverse the splanchnic nerves and sympathetic trunks. Some of these fibers pass directly to the adrenal from the splanchnic nerve, without first passing through the coeliac plexus. The parasympathetic nerves to the adrenal are usually derived from the dorsal vagus cord (Figs. 1 and 2) and sometimes from the anterior vagus cord also. According to Kure, spinal parasympathetic fibers pass to the adrenal through the splanchnic nerve. The vagus fibers may either pass directly to the adrenal or they may first traverse the coeliac ganglion (Fig. 1). Some authors deny the distribution of vagus fibers to the adrenal gland. Fibers to the adrenal from the phrenic nerve, as well as from an epiphrenic ganglion, have been described.

Histologically, a capsular plexus containing ganglia (Fig. 3) has been described. While some investigators have found nerves in the adrenal cortex, others deny their presence. There is complete agreement on the extensive innervation of the cells of the adrenal medulla. The presence of nerve cells is not a consistent feature. There is only a paucity of anatomical data on the innervation of the adrenal vessels.

Owing to the present war conditions the author has been unable to see his paper in galley proof.

LIST OF LITERATURE

- ALEXANDER, C. 1892. Untersuchungen über die Nebennieren und ihre Beziehungen zum Nervensystem. *Beitr. z. path. Anat. u. z. allg. Path.*, B. 11, S. 145-197.
- ALPERT, L. 1931. The innervation of the suprarenal glands. *Anat. Rec.*, vol. 50, pp. 221-234.
- ANDERSSON, O. A. 1894. Zur Kenntniss der Morphologie der Schilddrüse. *Arch. f. Anat. u. Entwicklungsgsch.*, Anat. Abt., S. 177-224.
- AREY, L. B. 1930. Developmental Anatomy. W. B. Saunders Co., Philadelphia, pp. 173.
- BIEDL, A. 1897. Beiträge zur Physiologie der Nebenniere. Erste Mitteilung. Die Innervation der Nebenniere. *Arch. f. ges. Phys.*, B. 67, S. 443-483.
- BRAUECKER, W. 1927. Der Brustteil des vegetativen Nervensystems und seine klinisch-chirurgische Bedeutung. *Beiträge z. Klin. d. Tuberc.*, B. 66, S. 1-65.
- BRÄUS, H. 1924. Anatomie des Menschen. Julius Springer, Berlin, B. 2, S. 234.
- BRIAU, E. 1897-98. Recherches anatomiques et physiologiques sur l'innervation du corps thyroïde. Thèses: *Faculté de Médecine et de Pharmacie de Lyon*, T. 2, pp. 1-65.
- CRILE, G. W. 1931. Recurrent hyperthyroidism, neurocirculatory asthenia, and peptic ulcer. *Jour. Am. Med. Assoc.*, vol. 97, pp. 1616.
- DOGIEL, A. S. 1894. Die Nervenendigungen in den Nebennieren der Säugethiere. *Arch. f. Anat. u. Phys.*, S. 90-104.
- DREYER, G. P. 1898-99. On secretory nerves to the suprarenal capsules. *Am. Jour. Phys.*, vol. 1, pp. 203-219.
- EDWARDS, L. F., and R. C. BAKER. 1940. Variations in the formation of the splanchnic nerves in man. *Anat. Rec.*, vol. 77, pp. 335-342.
- ELLIOTT, T. R. 1913. The innervation of the adrenal glands. *Jour. Phys.*, vol. 46, pp. 284.
- FUSARI, R. 1891. De la terminaison des fibres nerveuses dans les capsules surrénales des mammifères. *Arch. Ital. d. Biol.*, vol. 16, pp. 262.
- GOLOUBE, D. S. 1934. (Quoted from Goloube, 1936). L'innervation de la glande surrénale chez l'homme (étude embryologique). Recueil des travaux de l'institut psycho-neurologique de l'Académie des Sciences de la Russie Blanche, T2.
- , 1936. Sur le développement de la glande surrénale et de ses nerfs chez le poulet. *Annales d'Anatomie pathologique.*, T. 13, pp. 1055-65.

- GOTTSCHAU, 1882. Über Nebennieren der Säugethiere, speciell über die des Menschen. *Sitzungsb. d. phys.-med. Gesellsch. z. Würzburg*, S. 56-62.
- GREVING, R. 1931. Allgemeiner Aufbau und makroskopische Anatomie des vegetativen Nervensystems. L. R. Muller's Lebensnerven und Lebenstrieb. Julius Springer, Berlin, S. 3-10.
- HALLER, A. VON. 1766. *Elementa Physiologiae Corporis Humani*. Lausanne.
- HALLION, L. 1921. Réaction Vasomotrice de la Surrénale à l'Adrenaline. *Comp. rend. Soc. Bio.*, T. 73, pp. 146-9.
- HINSEY, J. C. 1933. On the absence of spinal parasympathetic fibers in the dorsal spinal nerve roots in the cat. *Am. Jour. Phys.*, vol. 105, pp. 51-52.
- HIRT, A. 1924. Vergleichend-anatomische Untersuchungen über die Innervation der Niere. *Zeit. f. Anat. u. Entwicklungsgesch.*, B. 73, S. 621.
- . 1930. Zur Innervation der Niere und Nebenniere des Frosches. *Zeit. f. Anat. u. Entwicklungsgesch.*, B. 91, S. 580-593.
- HOLLINSHEAD, W. H. 1936. The innervation of the adrenal glands. *Jour. Comp. Neur.*, vol. 64, pp. 449-467.
- , and H. FINKELSTEIN. 1937. Regeneration of nerves to the adrenal gland. *Jour. Comp. Neur.*, vol. 67, pp. 215-220.
- HOSHI, T. 1927. Morphologisch-experimentelle Untersuchungen über die Innervation der Nebenniere. *Mitt. s. allg. Path. u. path. Anat.*, B. 36, S. 328.
- HOVOLACQUE, A. 1927. Anatomie des nerfs graniens et rachidiens et du système grand sympathique chez l'homme. Gaston Doin et Cie, Paris, pp. 215-216.
- HUBER, G. C. 1930. Piersol's Human Anatomy. J. B. Lippincott Co., Philadelphia, pp. 1272.
- IWAMA, Y. 1925. Untersuchung über die periphere Bahn des Nervus vagus. II. Mitteilung: Über den gegenseitigen Austausch der markhaltigen Nervenfasern der beider-seitigen Vagi am Brustteil. *Fol. Anat. Jap.*, B. 3, S. 281.
- JACKSON, C. M. 1925. Morris' Human Anatomy. P. Blakiston's Son and Co., Philadelphia, pp. 987.
- JACOB, C. 1892. Beiträge zur physiologischen und pharmakologischen Kenntnis der Darmbewegungen mit besonderer Berücksichtigung der Beziehung der Nebenniere zu denselben. *Arch. f. exp. Path. u. Pharm.*, B. 29, S. 171.
- KOLLMAN, J. 1860. Über den Verlauf des Lungenmagenervens in der Bauchhöhle. *Zeit. f. wissenschaft. Zoologie*, B. 10, S. 413-448.
- KOLMER, W. 1918. Zur vergleichenden Histologie, Zytologie und Entwicklungsgeschichte der Säugetiernebeniere. *Arch. f. Mikroskopische Anat.*, B. 91, S. 1-139.
- KOLOSSOW, N. G. 1930. Zur Frage der Innervation der Nebennieren. *Zeit. f. Mikroskop. Anat. Forsch.*, B. 20, S. 107-121.
- KUNTZ, A. 1929. Autonomic nervous system. Endocrine and sex gland innervation. Lea and Febiger, Philadelphia.
- . 1938. The structural organization of the celiac ganglia. *Jour. of Comp. Neur.*, vol. 69, pp. 1-12.
- KURE, K., K. ICHIKO, and K. ISHIKAWA. 1931a. On the spinal parasympathetic. III. Physiological significance of the spinal parasympathetic system in relation to the digestive tract. *Quart. Jour. of Exp. Phys.*, vol. 21, pp. 1-20.
- , R. IKEDA, K. ICHIKO, and Y. WADA. 1931b. On the spinal parasympathetic. V. Physiological significance of the spinal parasympathetic. The spinal parasympathetic as vasodilator for the stomach and intestines. *Quart. Jour. of Exp. Phys.*, vol. 21, pp. 119-122.
- , Y. NITTA, M. TUZI, K. SIRAISI, and B. SUYENAGA. 1928. Demonstration of special parasympathetic nerve fibers in the dorsal or posterior roots of the lumbar region of the spinal cord. *Quart. Jour. of Exp. Phys.*, vol. 18, pp. 333-344.
- , Y. WADA, and S. OKINAKA. 1931c. The spinal parasympathetic. VI. The nerve supply of the suprarenal gland. *Quart. Jour. of Exp. Phys.*, vol. 21, pp. 227-241.
- , G. SAEGUSA, K. KAWAGUCHI, and K. SHIRAISHI. 1930. On the parasympathetic (spinal parasympathetic) fibers in the dorsal roots and their cells of origin in the spinal cord. *Quart. Jour. of Exp. Phys.*, vol. 20, pp. 51-66.
- , ———, and K. YAMAGATA. 1931d. On the spinal parasympathetic. Fourth article. *Quart. Jour. of Exp. Phys.*, vol. 21, pp. 103-118.
- LATERJET, A. 1930. L. Testit's Traité d'Anatomie Humaine. Gaston Doin et Cie., Paris, vol. 3, pp. 175.
- , et P. ROCHET. 1923. Précis-Atlas des Travaux. Pratiques D'Anatomie. Gaston Doin et Cie., Paris, 200, 202.
- MAYCOCK, W., and T. S. HISLOP. 1939. An experimental investigation of the nerve supply of the adrenal medulla of the cat. *Journ. of Anat.*, vol. 73, pp. 551-59.
- MCCREA, E. D. 1925. The abdominal distribution of the vagus. *Jour. of Anat.*, vol. 59, pp. 18-40.
- MOERS, A. 1864. Ueber den feineren Bau der Nebenniere. *Arch. f. Path. Anat. u. Phys. u. f. klinische Med.*, B. 29, S. 336-359.
- NAGEL. 1836. Ueber die Structur der Nebennieren. *Arch. f. Anat., Phys. u. wissenschaft. Medicin.*, S. 365-383.
- NISHI, N. 1909. Über den Mechanismus der Diuretinglykosurie. *Arch. f. exper. Path. u. Pharmacol.*, B. 61, S. 401-417.

- NOELLNER, F. 1869. Die Anatomie des Splanchnicus und der Nierennerven beim Hunde. *Beit. z. Anat. u. Phys.*, B. 4, S. 137-151.
- NONIDEZ, J. F. 1931. Innervation of the thyroid gland. I. The presence of ganglia in the thyroid of the dog. *Arch. of Neur. and Psych.*, vol. 25, pp. 1173-1190.
- . 1932. Distribution of the nerves in the thyroid of the dog. *Anat. Rec.*, vol. 52, pp. 28.
- PINES, L. and K. NAROWTSCHATOWA. 1931. Über die Innervation der Nebennieren. *Zeit. f. mikr.-anat. Forsch.*, B. 25, S. 518-538.
- POPOW, N. A. 1928. Über die Innervation der Glandula thyroidea beim Menschen und bei Säugetieren (II Mitteilung). *Zeit. f. d. ges. Neur. u. Psych.*, B. 115, S. 131.
- RENNER, O. 1914. Die Innervation der Nebenniere. *Deutsches Arch. f. klin. Medizin*, B. 114, S. 473-83.
- . 1931. Die Innervation der Nebenniere. L. R. Muller's Lebensnerven und Lebenstrieb. *Berlin*, S. 635.
- RHINEHART, D. A. 1912. The nerves of the thyroid and parathyroid bodies. *Am. Jour. Anat.*, vol. 13, pp. 91.
- RINDT, R., and R. H. KAHN. 1929. Über die experimentellen Grundlagen der Anschauung von direkten Beziehungen des Adrenalins zu den Nerven im Marke der Nebennieren. *Endokrinologie*, B. 4, S. 413-420.
- ROBINSON, A. 1925. *Cunningham's Text Book of Anatomy*. Wm. Wood and Co., New York, pp. 700.
- . 1931. *Cunningham's Text Book of Anatomy*. Wm. Wood and Co., New York, pp. 708.
- SCHKAWEA, G. L., and A. I. KUSNETZOW. 1923. Versuche an isolierten Nebennieren. *Zeit. f. d. ges. Exp. Med.*, S. 38, S. 37-66.
- SWAN, J. 1834. A Demonstration of the Nerves of the Human Body. Logman, Rees, Orme, Brown, Green, and Longman, London, pp. 51.
- SWINYARD, C. A. 1937. The innervation of the suprarenal glands. *Anat. Rec.*, vol. 68, pp. 417-429.
- TEITELBAUM, H. A. 1933. The nature of the thoracic and abdominal distribution of the vagus nerves. *Anat. Rec.*, vol. 55, pp. 297-317.
- . 1934a. The innervation of the thyroid gland. *Bull. Sch. Med., Baltimore*, vol. 18, pp. 77-91.
- . 1934b. The bilateral vagus innervation of the suprarenal glands. *Bull. Sch. Med., Baltimore*, vol. 19, pp. 24-25.
- , and E. UHLENHUTH. 1932. The mediastinal ganglion and its relation to the innervation of the thoracic viscera. *Anat. Rec.*, vol. 52, pp. 241-251.
- TOURNADE, A. 1925. La fonction adrenalinogene des surrenales. *Jour. méd. franç.*, T. 14, pp. 206-217.
- , et H. HERMANN. 1928. Chloralose et adrenalinosecretion. *Compt. Rend. Soc. Biol.*, T. 98, pp. 306-308.
- UCHIDA, S. 1928. Beiträge zur Kenntnis der Anatomie der peripheren Bahn des Nervus vagus. Über den Ramus suprarenalis N. vagi. *Acta Scholae Med., Kioto*, vol. 10, pp. 481.
- VESALIUS, A. 1725. *Opera Omnia Anatomica & Chirurgica*, vol. 1, pp. 399.
- WALTER, J. G. 1783. *Tabulae Nervorum Thoracis et Abdominis*. *Berolini.*, p. 15.
- WERTHEIMER, M. E. 1901. Sur les anastomoses réciproques des deux pneumogastriques dans le thorax chez l'homme, T. 53, pp. 832-834.
- WILLIS, T. 1720. *Opera Omnia*. Joannem Malachinum, Venice.
- YOUNG, B. Z. 1938-9. Partial degeneration of the nerve supply to the adrenal. A study in autonomic innervation. *Jour. of Anatomy*, vol. 73, pp. 540-550.





THE INTEGRATION OF VEGETATION

By W. F. GERICKE

INTRODUCTION

CONFORMATION expresses the adaptation of the plant to its environment. The multiplicity of species and varieties expresses the adaptation of vegetation as a whole to the diversities of soil and of climate. Integration of vegetation into a unity concept of adaptation, of form, of mineral absorption, of photosynthesis, and of crop-production per unit area exposure to sunlight is based on features that express the dependency of various plant parts on each other, but particularly the organs that absorb mineral nutrients and those that produce organic food for the roots. Conformation of plants changes with their advance in age. The features whereby species are arranged into an orderly assemblage of gradations, of continuities, and of harmonies to a cosmic surrounding express this dependency progressively with age and with changes in environment. The features which express the dependency of photosynthesis on the mineral absorption, and vice-versa, the mineral absorption on photosynthesis, are the primary elements for integration. They follow a common pattern of change in all plants, with climate as the chief cause of plant distribution. With the roots of plants obscured in the soil this pattern of change with climate could not be observed with sufficient clarity to integrate vegetation, but in hydroponics, with the growing roots visible so that they could be seen and studied, the results obtained in the last few years, from hydroponicums located in different climates, have now yielded the needed information for the integration of vegetation.

The conformation of a plant expresses the differences in the rates of growth of its parts. As plant distribution and culture are oriented by what climate permits, the rates of growth of the parts at different temperatures and light intensities hold the key to integration. Temperature and light are the primary cosmic forces influencing certain chemical reactions fundamental in the origin of biologic forms and in their adaptation to various regions. Form reflects the character of a plant's

mineral nutrition and photosynthesis, and thereby the yielding capacity of agricultural crops per unit area of surface exposed to sunlight. The integration of vegetation is based on the effects the primary cosmic forces have on the features which express the dependency of photosynthesis on mineral nutrition, and mineral nutrition on photosynthesis. Placing species according to the amounts of mineral nutrients absorbed per plant per unit weight of plant and per unit area, also according to the amounts of sugar, starch, protein, and other products produced, the orders reveal progressive gradations in root and leaf characters which show both their interdependent and complementary relations.

Conformation of plants is expressed by the ratios of the parts to each other

Conformation is expressed by using plant parts as the standard of comparison, expressing the measurements as ratios instead of as single dimensions. The dependency of photosynthesis on the mineral nutrition, and vice-versa, is implied by the ratio of root characters to that of tops. Species can be segregated into an array of categories by ratios such as weight of roots to tops—root diameter to leaf width—root diameter to total leaf area—root diameter to stem diameter—root spread to top spread—length of growth period of roots to total growth period of plants—and others. Closely allied species of similar leaf type such as wheat, oats, barley, rye, rice, corn, and sugar cane can be arranged in order of yielding capacities, amounts of mineral nutrients absorbed, and other characters, by one feature only, such as the ratio of root diameter to leaf width. Several features are required to place the species of dissimilar types in the order of their yielding capacities and mineral absorption. A low weight ratio of roots to tops indicates low mineral absorption as the intake of nutrients is conditioned by root growth. However, mere root growth among vegetation at large is, in itself, not a measure of the amount of mineral nutrients absorbed. Some species of high root-top ratio have low mineral absorption. No rapidly growing species of low root-top ratio such as water-

melon, and other vine crops, has high mineral requirement or absorption, but slow growing ones such as desert species might have. Vine crops usually require very rich soil to compensate for the low absorptive capacities of the roots.

Temperature and light affect the ratios of root to top growth

It is common knowledge that roots cannot stand as high temperatures as the leaves, hence the lowest root-top weight ratio for any species prevails in the hottest climate in which it can be grown, while on the other hand the highest root-top weight ratio is attained in cooler climates for which the species is adapted. The highest mineral absorption per plant corresponding to the largest root growth is in the cooler climate, but due to restriction of growth at highest temperature, the amount expressed as per cent might not show this difference, and in some plants might be higher for certain elements. The highest root-top ratio does not always prevail at the lowest growth temperature for all plants, for the roots of some species can not stand as cold temperature as the leaves.

The effect of increasing light intensities on root growth is different from that of temperature. Highest root-top ratio prevails where light is adequate for maximum photosynthesis, which for all high energy crops is full exposure to the summer sunshine. Lowest root-top ratio prevails where light is inadequate for maximum photosynthesis, but still adequate for foliar growth without leaves losing any color when the plants are grown at normal summer temperatures. Under such inadequate light conditions, leaves attain very large size but lack or are low in sugar or starch. The largest quantity of sugar in sugar beets, the largest amount of starch in wheat, the sweetest tomatoes, and the sweetest fruits of vines or trees are never produced by plants which have the largest leaves the species can produce. The largest yield of starch, sugar, or protein per unit area is obtained under light conditions which cause a moderate restriction from the maximum leaf size which the species is genetically capable of producing. This is in conformity with the laws governing plant conformation. It is a factor to be considered in the integration of vegetation into a unity concept of adaptation to its environment.

Species of the same general leaf-type and root growth can be placed in order of the yielding capacities for starch or sugar per unit area by the

ratio of root diameter to leaf width. The order for the largest yield per acre of the seven important members of the grass family is sugar cane, corn, rice, barley, wheat, oats, rye. It is significant in the study of adaptation, but must be passed here without comment, that the largest yields of each of these crops reported for the northern hemisphere were obtained in the northern half of the latitudinal zone in which the crop is grown. The order of the production data of the seven crops stated above is in agreement with the placement of the species by the diameter of the thickened roots, which convey organic food to the younger, thinner, and more remote mineral absorbing roots. It is also in agreement with the placement of the species for leaf surface per unit area of earth surface exposed to sunshine. However, these crops have different lengths of growth periods, but arranging the production data for an equal length of time the order is corn, sugar cane, rice, barley, wheat, oats, rye, and is in general agreement with placement by leaf width except for oats, which should stand before wheat. There is, however, overlapping of varieties, particularly rice, barley, wheat, and oats, when placement is by leaf width only, but considering only those varieties which are best suited for the general area in which the crop is grown extensively, leaf width indicates the relative productive capacity of each species. Varietal characteristics that cause overlapping when placement is by one feature only, however, gave the key to integrate other groups of vegetation, for variation in one character has correspondence in another which can be traced in the varieties of the same species.

Placement of principal crops of grass family for various characters by root to top ratios

By the law of conformation in plants, one dimension indicates others. Leaf width in cereals gives an approximation of the total leaf area of the species. Similarly, the thickness of the roots conveying organic food in the upland cereals gives a measure of the spread of their mineral absorbing roots. The largest amount of nitrogen absorbed from an acre of land by the crop of widest geographic distribution was from the largest yield of wheat which was approximately 7500 pounds of grain. The root-leaf features of this crop give the basis for comparison of absorption of this element by other species. As the diameter of the roots conveying organic food to the mineral absorbing

roots increases in barley, rice, corn, and sugar cane the per cent nitrogen in the plant becomes smaller but the total amount absorbed may be the same, larger, or smaller, depending on size of the plant. The corn plant absorbs much more nitrogen than the wheat plant because it has more root area of the same diameter and character as wheat. Rice and barley which do not exceed wheat in size have less nitrogen per plant, but varieties of both, having large tillering capacities, do absorb more than those wheat varieties which tiller sparsely. As the diameter of the roots conveying organic food decreases in rye and in the species of all other groups of vegetation, the per cent nitrogen in the plant, or the total quantity absorbed per unit area of land, decreases. Rye has the narrowest leaf, and the lowest leaf area per unit height of plant, of the common cereals extensively grown. Rye grain varies least in nitrogen of the high protein cereals. Emmer, a wheat, has narrow leaves and likewise varies little in protein compared to the broader-leaved bread wheats. Oats varies considerably in leaf size and root diameter, which is reflected by variation in the nitrogen content of the grain. Wheat has the greatest range of variation in per cent and amount of protein in the grain of all cereals as the protein may constitute from 6 to 28 per cent of the weight of the seed. Species of large roots such as corn vary less in nitrogen than those having smaller root diameter, but very fine roots do not have high absorptive capacity for nitrogen and hence variation is small in such cases.

Effect of root and leaf characters on the variation of protein in the cereals

Every species and variety has a minimum or irreducible per cent of nitrogen and of each of the other nutrients below which the plant or its products can not exist. Variation in the per cent protein of any species or variety can be expressed as the quantity of nitrogen absorbed above the plant's minimum requirements. Variation in per cent protein is due to those quotas of nitrogen absorbed during the latter growth stages of the plants as that which is absorbed early functions for maximum vegetative enlargement, which is the complement of the minimum. Withholding nitrogen from the culture media during the latter growth stage of wheat results in large yields of low protein, well filled, high starch content grain. Maintaining ample supply throughout the entire

growth period results in high protein grain with lower starch content. Similar treatment of rye or rice has little or no effect in changing the nitrogen content of the grain. The narrow-leaved rye and its smaller leaf area per unit height of plant restricts photosynthesis compared to that of wider-leaved species and consequently the amount of organic food for the absorbing roots. The absence of thickened roots which convey organic food precludes large spread of the finer roots and lessens the plant's absorbing capacity. Significant differences in thickness of roots usually do not show in seedlings a few weeks old, but show when the plants are in full vegetative vigor and greatest photosynthesizing capacity. In laboratory studies where plants were grown under glass in small containers of nutrient solution these differences could not show up because of limited photosynthesis. Rice has the thickest roots of all the small grain cereals but has very limited spread of fine roots of the diameter of those of wheat when the plants obtain full size. Consequently, rice generally is the highest in per cent starch and lowest in per cent protein of the cereals. In certain varieties where this may not hold, the explanation lies in the smaller diameters of the roots and narrower leaves. By proper grouping of plants, thickness of roots can be used as a measure of the quantity and quality of mineral absorption of different species and varieties. Rice grown in water submerged fields or paddies has the lowest root-top ratio and the lowest mineral absorption of the cereal crops. Corn has the greatest spread of fine roots of the diameter of those of wheat which bear from the thickened roots. It exceeds all cereals and sugar cane in photosynthetic power, mineral absorption, and protein production per plant. Sugar cane has the largest spread of thickened roots of this group of plants. They drive deeply into cooler soil below, overcoming the effect hot climate has on the root-top ratio of finer rooted plants.

When species of similar leaf types having moderate rates of growth are arranged in the order of increase in leaf size, their starch and sugar production per unit area of earth's surface increases, and conversely, when they are arranged in descending order for leaf size, their protein content increases. These products are in part complementary, and the conditions favorable to a plant for high production of protein is unfavorable to its highest production of starch or sugar, and vice-versa. Plants high in starch, sugar, or protein

have relatively high root-top ratio and mineral absorption. Plants having low root-top ratio have correspondingly low mineral absorption and low production of starch, sugar, or protein per unit area.

The ratios of the diameters of the thickened roots to the widths of the leaves in the high energy plants of the grass family are narrow and essentially alike in all species, as the wider-leaved plants have correspondingly thicker roots. Similarly, other high energy plants, not members of the grass family, such as potatoes, likewise show the same general narrow ratio between leaf area for photosynthesis and volume of those roots that convey organic food to the mineral absorbing organs.

The ratios of leaf width or leaf area of plants low in starch, sugar, and protein production to root volume are different from those of the high energy crops and segregate into several categories depending on a number of circumstances that cannot be developed in this short paper. Plants of low photosynthesizing capacity obviously do not require thickened roots to convey organic food. Cabbage, celery and lettuce have much thinner roots than wheat that bear from the root crown or central branching tap root. Although they have many very fine roots their absorptive capacities are low and richer soil is required for good crops of plants in this classification than is the case with wheat or other high energy plants whose roots are thicker and have greater absorptive power.

Other categories of root to top ratios of plants

A second category of low energy content and low mineral absorption vegetation is rapidly growing species common to warm climate, such as watermelon and other vine crops. Rapid foliar growth limits the amount of photosynthetic materials available to roots, and too high soil temperature might also restrict their growth. The root-leaf features of this group of vegetation are large leaf area and small root volume for organic food. This restricts mineral absorption. The amount of carbohydrates produced by an acre of densely covered vine crop such as watermelon, pumpkin, or tomatoes is small compared to that of wheat, rice, or corn.

A third category of low energy content and low mineral absorption vegetation is typified by one of the worst weeds of agriculture, a convolvulus, commonly known as morning glory or bindweed.

It gives the pattern for the root-leaf features for perennials, including trees. Integration of perennials involves consideration of the relation of starch, sugar, and protein to the production of cellulose, a subject that will be treated in other papers. The ratio of root-leaf features of convolvulus are essentially opposite to that of the other low energy group above mentioned. Perennials are dependent on the storage of a large part of the products of photosynthesis for renewed growth the next season. This requires a moderate rate of growth so that photosynthetic products may accumulate for storage. The pernicious habit of convolvulus is its moderate rate of growth whereby much of the products of the leaves are made available to the buds in the roots. The ratios of the root-leaf features of this category of vegetation are those of relatively small photosynthesizing area, and large root volume. Progressive increase in root volume with growth implies additional need for organic food or increase in leaf area. A moderate rate of increase of photosynthesizing area integrates into species with small leaves or a slower rate of growth than those having large foliage. Species having a moderate rate of foliation store more organic food in the roots than those having a high rate.

A fourth category of low energy content vegetation has very high mineral content due to its low rate of vegetative enlargement and long period of mineral absorption which is characteristic of desert vegetation. Integration of this group is oriented from the standpoint that these plants are repositories of inorganic elements rather than of the organic compounds which are the bases for the other categories.

Relations of rate of growth of plants to the production and storage of starch, sugar, and protein

Highest sugar or starch production per plant or per unit area requires a moderate rate of growth of vegetation. Too slow growth limits leaf area, that is photosynthesizing surface, and too rapid growth either of roots or leaves uses the products for vegetative enlargement thus leaving little for storage. Protein production also is influenced by rate of growth, but not as pronouncedly as starch or sugar. Slow growth, small leaves, and highest per cent protein in seedlings—that is, the small stunted state of vegetation—are associated phenomena. However, a large amount of protein production per unit area is dependent on con-

tinued growth of plants but too rapid vegetative enlargement dilutes the per cent by increasing the size of the plant—that is the area of production. Within the scope of these circumstances lie the factors for integration of vegetation for form which expresses the plant's adaptation to the circumstances of environment. Form is the means whereby the rate of growth of plants is adjusted to cosmic forces which affect fundamental chemical reactions. Rate of growth integrates into time required for a plant to produce a given amount of starch, sugar, protein, or their equivalents in other botanic products. The conditions whereby the highest amount of starch, sugar or protein are produced are the bases from which other cultural conditions are oriented. Only after mineral absorption, but particularly nitrogen, has declined either by depletion in the soil or by stoppage of new root growth, or unfavorable conditions to vegetative growth, can starch or sugar accumulate in high energy crops. The amount which the plant stores within itself depends on the leaf area and the length of period following the cessation of vegetative growth before the decline of the foliage. Protein does not accumulate in the plant after the absorption of nitrogen ceases—or otherwise expressed, when vegetative enlargement has stopped. The distinction between the conditions for high protein and high starch or sugar production per unit area is that the one is dependent on continued vegetative growth, the other on ample vegetative enlargement during the early growth stage followed by a long period when the leaves are active in photosynthesis only. Protein production is essentially a process of youth of the foliage, that of starch or sugar one of maturity. Protein production can be integrated into the length of time the foliage of a species is in a state of youth, that of sugar or starch into that when foliage is in a state of maturity, but does not include senility.

Plants can be segregated into categories by their root-top features, and species within each group arranged according to gradations based on the relationships that exist between (a) protein and carbohydrate synthesis, (b) protein production and rate of growth of plant, (c) sugar and starch production and rate of growth of plant, (d) protein production and length of the period of vegetative enlargement, (e) sugar and starch production and the length of time leaves are green but do not increase in size or number. The relations these various processes have one to another can be deduced from the conformation of the plants.

Using conformation as the basis on which to orient plants for the mineral needs, productive capacities of agricultural crops, and adaptation of species to their environment, vegetative features of plants are the means whereby the correlation of vegetation to its environment is established. Just to give an example of the profound interrelations of growth features in plants, a difference of one hour in the complete life span of two wheat plants of the same variety growing four months was detected by a corresponding difference in the composition of the grain. The higher per cent protein came from the plant which had the shorter life. The law of conformation requires that variation in one feature has a corresponding variation in another character.

The principles brought out in arranging high energy crops of the grass family for their productive capacities of starch, sugar, and protein apply to other categories of vegetation such as legumes, various classes of trees, warm weather plants, cold weather plants, those of low light requirement, those of high light requirement, and other groupings. Plants grown for products other than the primary energy materials, starch, sugar, protein, can not be placed solely by the amounts of these chemical compounds they contain. The relation these basic chemical compounds have to other botanic products, such as cellulose and water—the chief constituents of many species—must be considered in the integration. The dependency of root action on leaf action, and vice-versa, shows itself by distinguishing features. These show how species integrate into unity concepts of characters and of properties.

Wheat—the pattern plant by which other species are measured

The nitrogen requirement of species

A series of books is required to present this subject in completeness but a general idea of it can be obtained by consideration of some of the primary factors which segregate vegetation into categories and these into gradations by the features which express the species' requirements for each element. Integration requires use of features common to all vegetation for each element. The plant which has the greatest absorption gives the pattern of the features of that element which is to be integrated by the modifications which smaller quantities in other species manifest. Wheat has the greatest absorbing power for mineral nutrients

of the plants having the widest geographical distribution and can be taken as the basis from which other species are oriented. The root-leaf features of the crop giving the largest production on record gives the pattern of the mechanism which absorbed about 200 pounds of nitrogen from an acre of ground and produced 7500 pounds of grain. Seed is the chief repository of the nitrogen and phosphorus wheat absorbs. The seed-non seed ratio throws light on the character of the root-leaf dependence of various species and the distribution of nitrogen in the plant. The ratios of seed-non seed tissue cover a very great range among vegetation. Seed outweighs non-seed tissue in some species but in others is a negligible fraction of the weight of the plant. The ratio can be used as a yardstick to segregate vegetation into categories and determine whether or not the plant is an annual. All plants that have a high seed-non seed ratio are annuals but the converse, low seed-non seed ratio does not connote that all species belonging to this category are perennials. Perenniality is dependent on the storage of a considerable quantity of the plants' photosynthetic products, including some proteins, in the roots or in organs that will supply them later with organic food when growth is renewed. Storage of appreciable quantities of materials in other plant parts than seed reflects itself correspondingly by a lower seed-non seed weight ratio.

The amount of nitrogen stored in the seed is determined by the number, size, and composition of the kernels. Other things being equal, as the seed of other species of graminaceous crops increases in size above that of wheat the per cent nitrogen decreases, and as the size decreases the per cent nitrogen increases. The relations between composition and size in seeds of different species if properly grouped is similar to that of leaves. However, conditions are not equal, for diversity is the cause of species, and digression in the character of one feature of a given pattern is associated with covariation in other characters. For example, some rice seed is smaller than wheat, and also lower in protein. The integration of rice by the character of its seed involves the fact that the plant can not absorb as much nitrogen as wheat because of its lack of roots of requisite diameter and spread. Generally a large seed requires a longer time for filling with starch, sugar, or protein than a small seed. It is common knowledge clover seed requires but a fraction of the time from pollination to maturity that corn or wheat does.

The factor *time* integrates vegetation having a high seed-non seed ratio into that having a low seed-non seed ratio, or otherwise expressed, is one of the terms required to integrate annuals into perennials.

Similarly, as the conformation of the whole plant is the result of the interplay of various factors, so its parts such as the seed have their own distinctive conformations which likewise are the result of the interplay of various factors which can be integrated. In some cases the characters of comparable parts of species can not be interpreted except through the features of dissimilar parts. The integration of corn and clover by the physical characters of seeds, leaves, or roots only, is inconceivable, but the factor *time* by which species can be integrated for form unifies the diverse characters of these two plants so that they, like the pieces of a great jig saw puzzle, all fit into their proper places to complete the pattern of adaptation of vegetation to its environment.

Seeds of legumes are higher in per cent protein than the non-legumes, but when properly grouped follow the same general pattern as that of the cereal crops in the relation of change in size with per cent nitrogen. Likewise, their leaves when integrated to equal length of growth period follow the same general pattern in these features as that of graminaceous crops. Proper grouping of species is fundamental when arranging plants for their food requirements by one or more features which in themselves do not fully reflect the plants' conformation. Legumes have very wide geographic distribution—some are warm, others cold weather plants—some are annuals, others perennials—some have high, others low light requirement. The diverse characters of the legumes, notwithstanding the beclouding factor of symbiosis of the nitrogen-fixing bacteria, bring out some of the fundamental relations between (a) size and per cent protein, (b) age of plants and per cent protein, (c) length of growth period and per cent protein. The fundamental consideration in the integration of vegetation on the basis of starch, sugar, and protein production per plant and per unit area of earth's surface is to express the relation climate has to the production of these products, or, expressing the matter otherwise, to show how the latitudinal distribution of these products manufactured by different species integrates into the length of the period of favorable light and temperature. The basic pattern on which all vegetation is integrated for its geographic distribution is that the nearer

to the tropics the plant is grown, the longer the period of favorable light and temperature, hence longer growth period, hence more photosynthesis, hence more starch and sugar production per unit area per year. The converse to this is, the more remote from the tropics—that is, the nearer the pole—the shorter the period of favorable light and temperature, hence shorter growing period, hence less photosynthesis, but relatively more protein because short-lived species or annuals would be grown. Annuals are at home in the tropics also, where some have shorter, others longer growth periods, than those in cooler climates. The intensification of photosynthetic processes, which is an element that must be considered in the integration of species to climates, provides a shorter growing period, gives greater production per unit of time than in plants having a long growing period. A climate that favors perennial growth contains an element that operates against the accumulation of starch and sugar, for stoppage of vegetative enlargement is necessary for these products to accumulate as storage material. Stoppage of vegetative enlargement is also necessary for the production of high seed-non seed ratio in vegetation. As seed is higher in nitrogen than in any other part of the plant, it follows that the highest per cent protein a plant would have occurs during its seedling stage. The seedling stage of a plant's growth integrates into small stature vegetation. The greater the enlargement from the seedling stage, or the longer the life of the plant, the greater the decrease in per cent protein from that of its youthful state. The total amount of protein in the plant increases with growth, that is, with the absorption of nitrogen by the roots. When seed is produced, protein becomes localized and a new cycle of reactions begins with a new plant. A high seed-non seed ratio and a large production of seed per unit area by legumes require a moderate rate of vegetative growth. Peas are grown farther north and planted earlier in spring than beans. From the general pattern showing how starch, sugar, and protein production by the graminaceous crops, including sugar cane, vary with latitude, and from the general conditions governing the quantitative relation between protein and carbohydrate synthesis in any plant, the growth pattern for the cool weather peas and the warm weather beans can be deduced. Expressing this in a comparative way, cool weather for peas means slower growth, smaller leaves, smaller seeds which are higher in per cent protein, and lower in

per cent starch and sugar than beans. On the other hand cool weather also means longer growth period, hence lower per cent protein, and higher per cent starch and sugar than beans. Furthermore, it could also be interpreted to mean a lower light intensity which could restrict root action and the absorption of nitrogen. Due to these opposing circumstances it follows that some species and varieties of beans are higher in protein or have smaller seeds and leaves than peas. However, when all elements of conformation are considered, variation in one feature from the general growth pattern of a plant, which can only be stated by comparing it with that of another, has compensation in other features. These provide the earmarks by which diverse species can be integrated into unity concepts.

Plants low in starch, sugar, or protein which comprise many diverse species can be arranged in order of their absorptive capacities for nitrogen by the same tokens as the high energy and high protein plants. They are integrated and unified into a pattern which expresses the relation of rate of growth to form. Rate of growth can be used as an expression of the length of time required for the species to reproduce itself in seed or if a perennial store sufficient organic food in the roots for renewed growth the next season. Form integrates species into the chief elements of climate, light and temperature, by which all vegetation is oriented.

The integration of vegetation is based on a series of relations, each of which considered from a purely physical point of view is obvious. They are: The association of (a) rapid growth and large leaves or large size of plants, (b) slow growth and small leaves or small size of plants, (c) rapid growth and short life of plants, (d) slow growth and long life of plants, (e) rapid growth and coarse cellular texture in plants, (f) slow growth and fine cellular texture in plants, (g) rapid growth and little storage of starch and sugar in plants, (h) slow growth and small leaf area, hence little photosynthesis by plants, (i) perennial growth or long period of youth and short period of maturity of plants, (j) annual growth and relatively short periods of youth and of maturity, and others. All of these relations are influenced by cosmic forces chiefly temperature and light, which become expressed by the conformation of the plants.

Placing of the species for their requirements of other nutrients is in principle similar to that of nitrogen, but additional earmarks are required for each element. The nitrogen background is

necessary to orient each species, as it is the only soil element with minor exceptions that is a constituent of protein. The other elements become part of the mechanism which manufactures protein and carbohydrates, but are not raw materials out of which these products are made.

Calcium requirements of species

Calcium does not become localized in plants, consequently a ratio of high calcium-low calcium tissue can not be used as a basis for orientation as in the case of nitrogen. The chief function of calcium is in the structure of cell walls. Conceivably the more cell wall per unit volume of plant tissue, the more calcium the species require. Plants vary in their cell structure. The smaller the cells the more wall tissue is required per unit volume of cellular structure. The mathematical formula for the relation of surface area to volume with change in the diameter of particles gives an index to the ratio of amount of cell wall per unit volume of cellular structure of cells of different sizes. A structure composed of large cells gives a narrow ratio between their surface area and volume, and that composed of small cells has a wide ratio between these features. Wheat, rye and barley, when in full vegetative growth, have many more fine roots than rice, hence wide ratio between root area and root volume. These plants have much higher calcium requirement than rice as shown by the marked injury they suffer in culture solutions devoid of this element. Cabbage, low in protein, carbohydrates, and mineral nutrients, has many fine roots, smaller than those in wheat, and suffers markedly in calcium-free media. Sugar cane and orchard grass, low in per cent protein and fairly high in mineral nutrients, have thick roots which show markedly less injury in calcium deficient solution than plants characterized by high per cent protein or very fine roots. Associated phenomena among vegetation are (a) high protein, fine roots, and high calcium requirement, (b) low protein, low mineral content, very fine roots, and high calcium, (c) low protein, thick roots, and low calcium, (d) plants with pencils of unbranched roots, producing a narrow ratio of root area to root volume, and low calcium requirement, (e) vegetation with thick roots which penetrate deeply into soil layers richer in calcium than the surface stratum, with diverse calcium requirements depending on other features such as the fineness of the deep roots and protein content.

The root structures of plants having high calcium requirements suffer more injury from the lack of this element in the culture media than from that of any other element. As the root systems of species vary with the physical characters of the soil or culture solutions in which they are grown, so their calcium requirements vary. This affects the plant's tolerance for acidity. Many species have greater tolerance for acidity in liquid media than when grown in soils.

Potassium requirements of species

Species are arranged for their potassium requirements by tokens that integrate into the quantities of sugar, starch, and protein they produce. Plants high in any one of these products require more potassium per unit weight of growth than those that are not. The complex conditions under which various quantities of these products by the different species are produced, and the complementary relation between protein and carbohydrate synthesis, preclude placement of the species by their composition only. As the amounts of carbohydrates synthesized are influenced by light conditions, it follows that the plant's potassium requirement varies likewise. Potassium is required for vegetative growth. It has been pointed out that the productions of large amounts of sugar and starch are conditioned by the cessation of vegetative growth to permit these photosynthetic products to accumulate in plants. Certain light conditions can cause excessive vegetative growth and restrict photosynthesis so that starch and sugar do not accumulate in the plants. Such climatic conditions may increase the potassium requirements of plants by one process, but reduce it by another. Such opposing circumstances must be considered in placing species in the order of their potassium needs. The rôle of potassium in turgor and in the movement of water, processes influenced by climate, makes the plant's requirement for this element more subject to meteorological variations than any other of the major nutrients.

Potassium stands next to nitrogen in order of the amounts of nutrients absorbed from the soil except in vegetation adapted to very saline land. This element does not become localized in seed with the maturity of the plant as do nitrogen or phosphorus, consequently, the per cent potassium is lower at the seedling stage of growth than in later life, differing thus from those elements which accumulate in the seed.

The requirements of species for potassium in processes of which the highest performance of one can not occur under conditions essential for that of the other are reflected in root characters. Fine roots of the wheat type which have highest absorption of nitrogen, and the thick ones which convey the organic food of photosynthesis to them, are the elements out of which root characters are made. Thick roots extend the sphere of action of the thin ones. Increase in distance of these from the parts of the plants where they are used lowers their efficiency as food supplying organs. This affects the plant's potassium requirement as well as that of other elements from the standpoint of supply of the soil. Many combinations of these two elements of structure, thin and thick roots, are manifested by species. Diverse root structures are the adaptive features of diverse foliar structures.

It was pointed out that the ratio of leaf width to root diameter, or leaf area to root volume, was narrow among the high energy content species and that the ratio between these features was wide or otherwise distinctive in all of the low energy content plants. Within the scope of these relations lies the basis for arranging species for their potassium requirement. The amount of protein necessary for the production of a unit quantity of starch or sugar, and vice-versa, which varies among species, is a fundamental consideration in integrating plants for their potassium needs. The differences among species integrate into form, because of the relations rates of growth have to photosynthesis and the storage of starch and sugar. Other things being equal, the greater the production of protein, starch, and sugar per plant, or per unit area of earth's surface, the more potassium is required. As the amount of these products species produce would vary according to climatic factors, it follows that the potassium requirement would not be constant.

Magnesium requirements of species

Placing species according to their requirements for magnesium requires the background of the features associated with nitrogen, calcium, and phosphorus. Magnesium is a constituent of chlorophyll. It is also stored in the seed. The per cent is higher in the seeds high in protein than in those low in this product. In some species seed is richer in magnesium than in any other part of the plant, in others not. This places magnesium in another category from nitrogen and phosphorus,

which becomes localized in seed, and from calcium and potassium, which do not. Increase in leaf size among species connotes more magnesium for chlorophyll. Increase in per cent protein of seeds among species indicates correspondingly greater calcium and phosphorus requirements and, therefore, more magnesium. Increase of leaf size and per cent protein stand inversely related to each other so that the magnesium requirement of plants can be considered a balance between opposing circumstances. The lack of an element in culture solution whose function is for processes located wholly in the leaves, as is magnesium, has its counterpart in relatively more root growth than top growth. This gives the plants larger root-top ratio than where magnesium is available. This affects the composition of plants, which become richer in nitrogen and other elements than would be the case if magnesium were available. This explains some of the apparently inconsistent phenomena concerning the rôle of magnesium and the coloration of leaves. In some species lack of the element in the culture media is reflected in etiolation of the leaves, but in others deepens the green color. Species reflect gradations between opposing circumstances. Their diverse features may be considered as links of different sizes in the continuity chain of plant conformation. If a link is long, it also is narrow. Compensatory measurements are considered in using a plant feature as an indicator of the species requirement of an element. Provided the per cent chlorophyll does not change increase in leaf size among species means more magnesium. However, it also means more photosynthesis, and its converse, less protein. Thus, opposing factors determine the features by which the plants' requirement for magnesium is evaluated. The features are interpreted when resolved into their elemental components. Whether increase in leaf size and decrease in protein, or vice-versa, increase in protein and decrease in leaf size, was the more important consideration in determining a plant's requirement for magnesium is indicated by the shape and place of the link in the chain of continuity of species in plant conformation.

Phosphorus requirements of species

The placement of species in order of the quantities of phosphorus needed per unit weight of production requires the background of the features which indicate the plant's requirement for nitrogen

and calcium, also those which express the function of the element in the formation of nuclear proteids. Seed is higher in phosphorus than in other tissue, and thus the highest per cent in a growing plant would be found in the seedling stage. As the plant enlarges, the per cent decreases, but as growth is dependent on the absorption of more phosphorus the rate of decrease is not the mere complement of increase in size. Rates of absorption of phosphorus, and any other element, and vegetative enlargement are distinctive in their relationship one to another. The absorption of an element is dependent on that of other essential nutrients in the making of the normal plant which is distinctive in all of its phases of growth. The highest per cent of phosphorus in the seedling state of conformation, and the lowest at maturity state are the end points of a chain of gradations, each of which is distinctive in the general pattern of progressive change of plant conformation. The ratios of (a) girth to height of plant, (b) number of leaf buds to height of stem, (c) number of starting points for new roots to size of plant, are greatest in the seedling state of development. The ratios decrease as the per cent of phosphorus decreases with the age of plants. This gives the prototype for differences in the phosphorus requirements of species.

Plants having high protein and calcium requirements absorb more phosphorus than those low in this character. This relationship associates differences among plants in their absorptive capacities for phosphorus with those distinctive root characters that segregate species into groups for their nitrogen and calcium requirements. However, root characters alone are not sufficient to place all species. The range of variation in per cent phosphorus in the seed of a species is less than that of nitrogen, but may be greater in the non seed tissue. The absorption of phosphorus is not as closely adjusted to the physiological requirements of various processes of growth as nitrogen, and plants may absorb more than they need. The relation of excess absorption of an element to conformation is considered in the placement of species, but this subject is too long to be discussed in a short paper.

When the amount of phosphorus required for the maximum yield of wheat per acre is absorbed by an equal area of corn, the per cent in the plant is lower, because of the greater size. Corn absorbs more phosphorus than wheat so that the smaller per cent in the plant is associated with a larger quantity removed from the acre. The same

quantity in smaller plants would be reflected by a larger per cent of the weight of the vegetation, and by the features or conformation of the smaller plants. Similar principles hold for the relationship of composition to size in varieties but in order to place them for their capacities to absorb phosphorus, all elements of conformation must be used. The features of species and varieties are unified by integrating them to equality. Without integration, species are many ontogenies, but by integration they are merely different amounts of mineral nutrients absorbed by roots, and different amounts of photosynthesis by leaves for equal units of time. In order to place species according to the amounts of phosphorus they require per unit weight of growth, the features which indicate their requirements for nitrogen and calcium are integrated to show how these elements are related to the number of growing points species have. The more branches, leaves, and seeds per unit length of stem and the more root branches per unit length of main root, the more phosphorus species require.

Requirements for other elements

Species can be placed in order of their requirements for sulfur and iron by distinctive features.

The functions of the minor elements boron, manganese, zinc, and copper are not sufficiently clear to place species for their requirements of each of these elements. It is known that they vary and that climate affects the amount certain plants require of the various minor elements.

Mechanism of absorption and selection of elements by plants

The relation between thickness of roots and the quantities and qualities of elements absorbed suggests that the mechanism of selective absorption might be in the size of cells. Normally, the rapidly growing thick roots would have a coarser cellular structure than the slower growing fine roots. Nutrients are absorbed primarily in solution, but entry into plants of minute quantities of ions by emanation is not precluded. Osmosis conveys nutrients with water as it passes from the dilute soil solution to a more concentrated root sap. Osmosis varies with the concentration of cell sap and not with the thickness of root, hence, would not explain the selective absorption noted in the species of different root sizes. Nutrients can also enter with capillary movement of liquids along solid surfaces and the walls of porous bodies, such as plant cells. Movement of liquid by capillary

attraction in cellular structure orients the surface attraction forces according to the arrangement of the walls. The attraction of opposite walls of the cells for their fluid contents creates a boundary zone between liquid films where the resistance to the entry of materials is lowered by the pull of opposing forces. This affects the permeability of the wall and may allow ions that are not too large to pass through. Size and shape of cells determine the orientation of capillary attraction forces and the character of the boundary zone between opposing pulls. Histological data on roots of species are too incomplete to arrange plants by their cell patterns for correlation of the molecular dimensions of the nutrient elements with the character and orientation of surface tension forces in cell structure. The property of roots to absorb some elements and not others may conceivably show correspondence with cell size. Elements that enter would be of a size to conform to this boundary zone. The very large cells of species having thick, rapidly growing roots would have their walls too far apart from the opposing pulls to affect the permeability of the walls in the boundary zone. Very small cells would not have a boundary zone of adequate size to permit nutrients to pass through them. The fact that the greatest absorption of mineral nutrients by plants is not obtained by the thick roots or by very fine roots having a great absorbing surface is of consequence. Selective absorption of nutrients by plants appears to be a function of cell size.

Balance between opposing circumstances

The integration of vegetation for form brings out the relation and balance which opposing circumstances have on growth and accounts for the characters of species in their latitudinal and elevational distribution. Increase in temperature with the lengthening days of late winter and early spring and the decrease with the shortening days of late fall have two opposing factors affecting the root-top ratio of growth in plants. This meteorological effect is reflected geographically in the change in the root-top ratio of vegetation with latitude. The approach to the tropics tends to cause a low root-top ratio by virtue of increase in temperature, but a high ratio by that of light. The approach to the pole tends to cause a high root-top ratio by virtue of lower temperature, and a low ratio by that of light. Due to the inclination of the earth's axis, light becomes favorable to

growth in spring before temperature does, and remains so, longer in autumn. The nearer the pole the more pronounced are these circumstances with the change of seasons. They reach their climax in the longest days of sunshine of the short season of favorable temperature in the highest latitude vegetation grows. The integration of vegetation for form is oriented on the minimum time required for species to reproduce themselves by seed, or if perennials, by the storage of organic food needed for renewed growth the next season. Form integrates into the size the species attains within the time conditions are favorable to growth. Form, size, and length of growth are interrelated and interdependent one upon the other. For example, wheat and barley can reproduce themselves by viable seed in about six weeks after the seed is planted, or can require about ten months, depending on temperature and light conditions, and also at all gradations between these extremes. Obviously, wheat or barley plants that complete their entire growth cycle in six weeks are smaller and of different conformation than those which required longer time. Length of growth integrates into size and form, and each of these characters into the other. Light and temperature affect size, form, and length of growth period of species differently, as some have small, others large amplitude in which to adjust their growth cycles to the prevailing circumstances. Size and form integrate into rates of growth which integrate into the cosmic forces, temperature and light. Form, adaptation, mineral absorption, photosynthesis, and production of agricultural crops per unit area of surface exposed to sunlight are interrelated phenomena. The integration of vegetation for one of these subjects aids in that of another. None can be completely integrated without the other.

Hydroponics provided another ecology which made differentiation of edaphic and meteorological factors affecting plant growth possible

Hydroponics has provided the key to the source of, and the avenue for, the information needed to proceed with, and to complete the integration and the ordination of vegetation into unity concepts of each of the above subjects. This is a comprehensive undertaking. That soilless crop-production became the means to integrate soil vegetation is due to the fact that hydroponics provided a different ecologic basis and background than that

on which all vegetation is oriented. It was impossible with soil grown vegetation to differentiate edaphic and meteorological factors on growth. Only by the elimination of the soil in crop-production could the edaphic and meteorological factors be evaluated independent of each other. Plants have been grown extensively in small containers of nutrient solution for experimental studies in scientific laboratories since 1860. The primary object of these experiments, and the goal of soil science, generally, was to give chemical interpretation of the ways and means soils make plant foods available, and explain how vegetation uses them. The methods of study projected the nutritional features of plant growth into the foreground and relegated the climatic factors, which held the key to the origin and adaptation of species to their environments, into the background. Climate affects vegetation through the physical properties of the materials with which it is in contact. Those used in hydroponics may have markedly different climatic and ecologic effects than soil. Essentially hydroponics created a new order of climatic and ecologic environment in the culture of vegetation, which, like that of soil, is the basis on which the mineral nutrition of plants for water culture is oriented. A few degrees of temperature segregates the vegetation of different climatic zones. Because materials of low specific heat, such as vegetable litter used in hydroponic seed beds, would change in temperature quickly, certain orders of solar radiation can have categorical effects on vegetation grown by hydroponics that would not be the case with soil.

It is the ecology of root growth in liquid media that makes hydroponics a new science. Roots segregate plants into categories. Changes in the root types of species reflect themselves by other features. Liquid media markedly affect the root types of species by the elimination or restriction of features which make them different, such as thick storage roots, thus tending to make plants alike in their absorptive organs. This change of root types reflects itself in the much greater similarity of mineral composition of different species grown together in the same nutrient solution, than when grown together in the same soil. The fact that many species will grow equally well in the same nutrient solution but not in the same soil is further evidence that the change in root types will have corresponding effects in other features of the plants. The mineral and climatic requirements of the plants vary with their root

types which are the expressions of the adaptation of species to diverse soil and climate. The complete elimination of these diversities would project the plants to the influence of their original environment, that is, marine habitation. Root producing vegetation is autochthonous. As roots hold the key to the evolutionary adaptation of marine species to soil, so likewise, they hold it for cultural adaptation of autochthonous vegetation to hydroponics. The evolutionary history of vegetation from a pre-root state of marine habitation to the large roots of large trees growing at high elevation with its great extremes in climate aids in ordering vegetation for adaptation to hydroponics. When land species are grown in liquid media the root systems become markedly unified, as the thickest and the thinnest, the longest and the most branched organs, characteristic of their soil habitation, do not form in water. The significance and implication of an altered root system on the physiology of water grown vegetation is far reaching. The magnitude of change species undergo from soil to hydroponic habitation, and the amplitude of change they can undergo without harmful effects give the physiological background on which plants are ordered for water culture. Species can be integrated for hydroponic culture by root-top features for form, adaptation, mineral absorption, photosynthesis, production per unit area of earth's surface, similar as for their soil habitation. They segregate into categories for which appropriate cultural technique and conditions must be provided in order to grow them successfully without soil. A series of books, one of which is published, (*Complete Guide to Soilless Gardening*, 1940: Prentice-Hall, New York; Putnam, London. See also articles on Hydroponics, *Encyclopaedia Britannica Year Books*, 1939 and 1942), others being in the making, are required to formulate this subject into a useful compendium for those who wish to grow crops by this method. Mastery of the art and science of growing crops without soil consists in a great measure in understanding plants from the standpoint of ecology, which is different from that of agriculture.

The root-top weight ratio of plants grown by hydroponics is less than that of soil. This is significant in practical production, as the margin of safety and assurance against the event of untoward conditions arising is much less than with crops grown in soil. On the other hand, it has its advantages as plants having a low root-top ratio can be placed closer, giving a larger produc-

tion per unit area than in soil, provided the cultural technique is arranged wisely within the smaller amplitude of highly favorable circumstances to plant growth which water culture permits. A cubic foot of nutrient solution contains from three to six times more available water than a similar volume of various soils, therefore, certain crops such as potatoes and corn can be planted closer than in agriculture with corresponding increases in yield. There are crops that can not be planted closer in hydroponics than in soil because of the limitations of light, and there are species whose root structures make them unsuitable for water culture. In hydroponics, stand is determined primarily by light considerations; in agriculture it is by the amount of nutrients available in the soil. The area of earth's surface having favorable light and temperature for crop production is much greater than the area of arable land. Hydroponics can outyield agriculture both in the production per unit area for certain crops and in the extent of area where it can be employed. A discussion of the economics of this method of production is outside of the pale of this paper, but from the elements that determine cost it is evident that hydroponics will be an economic competitor to agriculture in some important lines of production.

Hydroponics has introduced some new problems of physiology and ecology arising out of the root action of plants, which affect the immediate surrounding climate more than in the case of soil grown vegetation. The plants lose more water by guttation—liquid issuing from the tips of leaves—which can have either harmful or beneficial effects, depending on circumstances. Great loss of water by guttation in greenhouses during winter can add to the burden of disease control, but air conditioning can overcome much of this difficulty. This property of plants, on the other hand, provides a natural means of air conditioning homes by providing more moisture in the atmosphere, especially desirable in winter when the air has become too dry from heating. Species vary in their transpiring and guttating power according to the characters of their leaves and roots. Vegetation can be integrated for its climate influencing properties by features that show the nature of the dependence of these organs one on another for intake and loss of water. Other properties of plants made manifest by hydroponics open new avenues to human interest. These, with those just mentioned, appear to herald an age when much smaller space and less mechanical and in-

dustrial organization will be required for man to enjoy his dependence on his own vine and fig tree.

Evolution of plants clarified by hydroponics

As hydroponics has provided a key for the integration of existing vegetation so likewise it has provided a key that will unravel some of the evolutionary history of past floras. The changes which the roots of species undergo in water culture from that of their soil types are *reversion* to primitive states in which they existed in their evolution from an original marine habitation through different stages of soil ecology consisting of marshes, lowlands, and highlands to the present status of land habitation with its great diversities of climate. Species adapted to uplands with great diversities of climate undergo much greater change in hydroponic culture than those adapted to lowlands with equable climate. Using integration as the means to arrange species for their evolutionary history, it can be shown that the vegetation of any geologic period, whose fossil remains or products are in existence, did not produce as much protein, or starch, or sugar, or cellulose, or lignin, or any plant product containing fixed carbon, or absorb as much of the soil minerals per unit weight of plant, per unit area of earth's surface, per unit of time than does the vegetation of today. The forms and features of past floras, the characters of the soils on which they grew, the kind of climate to which they were exposed, and some of the characters and features of the animals whose food these plants were, all unfold themselves by integration into a panorama of evolution where individual features can be deduced and evaluated by the relationship they as parts hold to others of an ordered cosmogony and a defined cosmography.

Comparison of the rate of carbon fixation by plants today with that of geologic times can be obtained by estimating the amount of coal which would be formed by the most rapidly growing species if such carbonization processes were possible now. More than one million board feet of lumber has been obtained per acre from some of the best stands of California coast redwood (*sequoia sempervirens*) averaging 500 years in age. This amount covers an acre with solid lumber 23 feet deep. Lumbermen state that about one half of the volume of these trees is used as lumber. Thus, the actual amount of woody tissue produced in 500 years would cover an acre twice the above figure. The density of bituminous coal ranges

from 1.2 to 1.5, and the best grades are from 80 to 90 per cent carbon. The density of redwood ranges from 0.7 to about 1.00 and pure cellulose is 40 per cent carbon. Four cubic feet of fairly dense redwood contains as much or more carbon than the average solid cubic foot of good bituminous coal. Forty generations of redwood, one succeeding another every 500 years, at the above rate of growth, continued for 20,000 years, would fix enough carbon in woody tissue to create a coal seam 500 feet thick which is more than the summation of the known coal seams laid down in geologic history, estimated at many millions of years. It is to be noted that these figures do not include the roots which in redwood range from 30 to 40 per cent of the weight of the tree when in active growth of vigorous youth.

Integration clarifies the properties of vegetation which became coal and explains why most dead vegetal tissue does not undergo carbonization today. Microorganisms cause disintegration of plant tissues which contain protein, starch, sugar and other materials as food to sustain their activities. These food materials for micro organisms were either lacking or present in insufficient quantities in ancient floras, hence they did not decay when dead, thus permitting accumulations of great thickness of vegetal material to be eventually submerged by water or soil or both for ultimate carbonization and solidification. Geologic plants did not have the kind of roots which were capable of high absorption of essential mineral nutrients, hence, they could not produce a foliage capable of the high rates of photosynthesis of today, and vice-versa, the photosynthesis then was not capable of sustaining a large root system. Ancient soils were not of a character conducive to produce a root system of high absorptive capacity of those elements necessary for high production. Also the genetic constitution of that vegetation was not developed to encompass physiological functions at high rates. Geologic history can be unravelled by the rate of change in the physical features of

plants in past ages which can be mathematically deduced, and employed in integration. This integration employs differentials derived from the projection of progressions of features and conditions which are known or can be experimentally established, and carries them to the ultimate goal.

Erroneous views concerning determining factors in soilless crop-production

Hydroponics has suffered harm and violence from misinformation, misconceptions, and various half-truths. Terms like *chemical gardening*, *chemical farming*, *chemiculture*, *nutrient culture*, *magic gardening*, etc. which directed attention to, and gave emphasis on the nutritional features of water culture, thereby relegating the far reaching, and determining factors of ecology which the new system and its equipment created, into the background, were most unfortunate. Books, bulletins, and reports have been published purporting to give directions on soilless plant culture without such important words as *climate*, or *ecology*, or any of the concepts they imply, appearing on their printed pages. It is probable that no individual has tested more chemical combinations in nutrient solutions for plant culture in laboratory studies along classical lines, and used greater numbers of cultures and species than the author, but the information that was most helpful to him in originating and establishing soilless crop-production came from observation and studies of plants in Nature's outdoor workshop. A naturalist's point of view was necessary to complement and fulfill the essence of a development that remained hidden in three quarters of a century's experimentation with water culture in academic studies. Practical working knowledge is made possible for all and the science of hydroponics is formulated by the integration of species, both for soil and for water culture. Integration answers questions of plant physiology and ecology which could not be resolved by other methods.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of THE QUARTERLY REVIEW OF BIOLOGY, Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore, Maryland, U.S. A.

BRIEF NOTICES

EVOLUTION

THE UPPER ORDOVICIAN FAUNA OF FROBISHER BAY' BAFFIN LAND. *Geology, Memoirs Field Museum of Natural History, Volume 2.*

By Sharat Kumar Roy. Field Museum Press, Chicago. \$3.50. 12½ x 9½; 212; 1941 (paper).

The records and material forming the basis of this report were collected during the season 1927 and 1928 by the geologist of the Rawson-MacMillan Expedition of the Field Museum to Labrador and Baffin Land. Baffin Land is a large, long, irregularly-shaped area lying above Labrador between northeast Canada and Greenland, closer to the Canadian shores, however, than to Greenland. Frobisher Bay, a deep indentation at the southeastern extremity of Baffin Land, and once thought to be the passage from the Atlantic to the Pacific, was the final destination of the Field Museum Expedition. The expedition was organized to spend two summers and a winter cruising in the coastal waters of Labrador and Frobisher Bay, making observations and collections relating to anthropology, botany, geology and zoology. For the geologist, Silliman's Fossil Mount, at the upper reaches of Frobisher Bay and the only sedimentary formation throughout this entire region, was the chief field of exploration.

In an introductory chapter the author gives an interesting outline of the journey. Three excellent maps furnish the reader with a clear picture of the numerous points touched. Fossils totalling to 92 species have been collected from the Mount, an isolated hill of limestone lying upon pre-Cambrian rocks, on three previous occasions. The much larger Field collection consists of 68 genera with 116 species, but Roy does not consider that he obtained all the forms present. The approach of winter hastened the expedition on its way. Among the forms listed are Receptaculites, corals, cystoid and crinoid, bryozoans, brachiopods, pelecypods, gastropods, cephalopods, trilobites, and ostracods. These are all described in detail and illustrated. In a "Synopsis of Fauna" Roy gives the geologic ranges of

North American and Greenland species allied to those from Silliman's Fossil Mount. There is also a discussion of previous collections from the Mount and an interpretation of the age of the fossil area. Regarding the age the author says:

The question at issue is whether the fossils from Silliman's Fossil Mount represent the Mohawkian (Black River and Trenton) or the Richmond or both.

The above statements afford the basis to conclude clearly that the Silliman's Fossil Mount fauna and its equivalents are a recurring Mohawkian fauna of early Richmond age. The facts that the elements with Mohawkian affinities in these faunas are rarely conspecific with typical Mohawkian species and that these faunas contain a considerable number of unquestioned Richmondian forms are alone sufficient evidence to arrive at such a conclusion.

On the northeast coast of Labrador, 22 drift fossils, representing four genera and six species of Hormotoma, indicate a much wider distribution of the northern Canadian faunas than was formerly thought.

The volume is beautifully printed and illustrated with many excellent photographs and figures and concludes with a bibliography of seven pages and a detailed index.



TRANSACTIONS OF THE AMERICAN PHILOSOPHICAL SOCIETY. *New Series, Volume XXXI, Part V.* Papers as follows: *The Anatomy of the Pelecypod Family Arcidae*, by Harold Heath. *The Brain and Its Role in the Phylogenetic Transformation of the Human Skull*, by Franz Weidenreich. *Phylogenetic and Cytological Studies in the Ranunculaceae*, by Walton C. Gregory.

The American Philosophical Society, Philadelphia. \$3.00. 11½ x 9; 287-520 + 34 plates; 1941 (paper). The family Arcidae (Ark-shells) is estimated to include not less than 1200 species, the majority of which are fossil forms and have been classified, as have many

recent species, on the basis of shell characteristics. Thirty-two species and subspecies are described by Heath. The author does not modify the existing scheme of classification but in the *Résumé* he discusses the changes that seem to be in order since "a scheme of classification based upon shell characters alone may lead to erroneous conclusions..." It is "equally evident that comparisons based upon a single organ or system may also prove to be untrustworthy." Twenty-two plates (6-15 figures each) illustrate many of the diagnostic features.

In the second paper Weidenreich finds that

Cranial sutures in recent man show a tendency to fuse relatively late in life when compared with anthropoids in which they close and even become partly obliterated shortly after the second dentition is completed. The suture of all the three adult *Pithecanthropus* skulls now available... exhibits such a state of closure as is scarcely attained in recent man, or if at all, at a rather advanced age.

An interesting comparison is made with the forms and proportions of the skull of the dwarf and large dog and other mammals, and the effect of the enlargement of the brain case and the reduction of the face on the palate and dental arch. We can only quote briefly some of Weidenreich's conclusions:

The phylogenetic evolution of the human skull is characterized by a continuous enlargement of the brain. The morphological effect of this enlargement corresponds completely in principles and details to that which is seen in the dwarf dog, as a consequence of its relatively larger brain.

The phylogenetic evolution of man, at least in its late phases is characterized by the absolute increase in brain size. The brain size, therefore, represents a character of the first order but all the peculiarities of cranium and face which result from the enlargement of the brain and are generally considered the most essential indicators of evolutionary progress are characters only of the second order... Since the enlargement of the brain appears as the inducing cause of other morphological alterations, the question is justified as to which general factor may now be made responsible for this enlargement... [It] is certainly in some way connected with the adoption of the erect posture and the corresponding transformation of the entire skeleton.

All the facts imply that phylogenetic evolution of man proceeds under the form of an orthogenetic development.

Forty-one tables of measurements and 56 figures are included in the text.

The last paper is concerned with the reclassification of the Ranunculaceae from the cytological standpoint. Type and number of chromosomes have been examined in 19 genera and 108 species. These results are given, and camera-lucida drawings of the chromosomes of all the species studied are arranged in 12 plates with 132 figures. The effect of polyploidy in the evolution versus the speciation of the family is discussed.

A phyletic rearrangement of the genera and tribes of the family has been made on the basis of chromosome-type, size, and basic chromosome numbers of the family. On the same data a polyphyletic origin of the various tribes of the family from some ancestral group has been suggested and has been illustrated by phylogenetic charts comparing the classical and the author's classifications.

All three papers are provided with reference lists.



MAN AND THE VERTEBRATES. *Third Edition, Revised.*

By Alfred Sherwood Romer. *The University of Chicago Press, Chicago.* \$3.50. 8 x 6½; viii + 405; 1941.

This book, since its publication in 1933, has found wide use as a text and reference book for college students in biology. It presents in a most interesting manner, an easily readable account of the origin and evolution of the vertebrates and a rather detailed survey of the structure and relationships of the primates and man. Although written with a minimum of technical language and detail, the work is comprehensive and authoritative and its usefulness is greatly enhanced by the excellent figures with which it is profusely illustrated.

This, the third edition, has undergone some revision and much new material has been added. One notable addition is the interpolation of a chapter on the anatomy of the frog designed to accompany laboratory dissection of this animal. The chapters dealing with fossil man and human races have been considerably altered and expanded and the sections on higher fishes have been completely rewritten. The material has been brought up to date by the introduction of discussions of new developments in the field, as for example, the recent discovery of a living coelacanth off the South African coast. An appendix giving a synoptic classification of the vertebrates and several phylogenetic trees has been added.

The format of the book has been greatly improved in this edition by having it reset in a more modern style and typography. The number of figures has been greatly increased and the excellence of the photographic illustrations has been brought out by printing them as plates rather than as text-figures. These plates are distributed in groups throughout the book. Unfortunately, the illustrations are not numbered, so that exact reference to them in the text is not possible. Since a single group of plates may deal with several different subjects which are discussed in separate portions of the text, the lack of figure numbers does seem to hamper the author in making full use of the illustrative material in the course of his discussions. It must be said, however, that this disadvantage is not serious and it is in fact partially offset by very full explanations in connection with each figure. The

former editions of Romer were excellent, the present one is even better.



THE MAMMALIAN FAUNA OF THE WHITE RIVER OLIGOCENE. Part V. Perissodactyla, by William Berryman Scott. *Transactions of the American Philosophical Society Held at Philadelphia for Promoting Useful Knowledge. New Series, Volume XXVIII, Part V.*

By William B. Scott and Glenn L. Jepsen. *American Philosophical Society, Philadelphia.* \$3.00. 11½ x 9; 747-980 + 22 plates; 1941 (paper).

Part V of this fine series of *Mammalian Fauna of the White River Oligocene* completes Volume XXVIII of *The Transactions*. Two suborders make up the order of Perissodactyla represented in the White River—the Chelopoda, normal perissodactyls with hoofs, and the Ancylopoda, in which the hoofs have been converted into claws. In modern times only three families of perissodactyls exist—horses, tapirs, and rhinoceroses. The old Tertiary of North America and Eastern Asia were the principal regions of perissodactyl development. Eight families are represented in the White River beds. Of these the brontotheres and heileletids came to an end within the White River age. The clawed perissodactyls are not found in North America after the upper Miocene.

The rhinoceroses reached their culminating point in development in North America in the White River, where they are represented by three families, and show more diversification than at any subsequent stage. They disappeared in the lower Pliocene. The tapirs are represented by a single family and genus in the White River and do not occur in abundance. However, Scott points out that their scarcity may be more apparent than real, due to conditions of fossilization, for they were probably then, as now, solitary forest dwellers. They persisted to the close of the Pleistocene. Horses during the Oligocene "were in a state of extraordinary development and diversification and that at a time when the family is not known to have been represented in any other continent. White River horses are surprisingly diverse, whether the many different forms are ranked as genera, species, or geographical races." In their evolutionary history horses are almost at the half-way stage in the White River beds.

Altogether Scott lists and describes about 75 forms of perissodactyls. Measurement lists, tabular matter, 157 text figures, and 22 plates are included. Part V also carries the table of contents and the index to the complete volume.



PALEOZOIC GASTROPOD GENOTYPES. *Geological Society of America Special Papers Number 38.*

By J. Brookes Knight. *Geological Society of America, New York.* \$4.50. 9½ x 6½; vi + 406 + 96 plates; 1941 (paper).

It is a good thing that some devotees of science are satisfied to give their time and energy to producing works of this sort. The digging up of ancient documents that have no merit whatever except age is tiresome in the extreme, but it is necessary in order to clear up the mass of nomenclatorial tangles that still seem to be accumulating faster than they can be assimilated. The only satisfaction that an author can take in a product of this nature is that he is smoothing the path for others who will come after him. That this kind of work is necessary is the result of carelessness on the part of other workers.

The present volume lists in alphabetic order over 500 generic terms, together with full synonymy and type designations. Where there has been more than one designation in the same genus, the reason for the selection is given as well as the present location of the original type specimen, if it is known. Similar works are urgently needed for the Mesozoic and Cenozoic and recent genera.

The 96 full-page photographic plates, the 7-page index, and the 28 pages of introductory material add greatly to the value of the volume.

In passing, it may be noted that the word "genotype" is of faulty etymology. Berry has pointed out that it should have been "generitype." The fact that this term is in use in genetics as the antithesis of "phenotype" makes the change of spelling of the taxonomic term desirable, but taxonomists are likely to adhere to the present spelling on the basis of their fifty-years priority over the geneticists.



GENETICS

MEDICAL GENETICS. A Series of Lectures Presented to the Medical Schools of Duke University, Wake Forest College, and the University of North Carolina.

By Laurence H. Snyder. *Duke University Press, Durham, N. C.* \$1.50. 7½ x 5½; viii + 130; 1941.

A result of a series of lectures delivered at the medical schools of Duke University and the University of North Carolina, Snyder's book is a condensed and remarkably clear survey of the present-day knowledge of hereditary pathological conditions in man. The author is convinced that, in spite of its incipient condition, medical genetics already is of practical value to the physician. The didactic qualities of his short account will undoubtedly help to convince the reader of the correctness of his view. The book will be appreciated, however, not only by readers whose main interest lies in the practical, more specifically medical aspect of genetics but by all students and teachers of genetics.

The latter will find it a useful addition to the existing sources of orienting information.

After presenting in the introductory chapter the various possible applications of medical genetics, explaining the generality of genetic principles and doing away with some traditional misconceptions concerning human heredity, the author proceeds to present two extreme categories of hereditary characters in man: (a) blood groups and blood types (Chapter 2: Medico-legal applications) as clear-cut cases of mendelian inheritance, and (b) mental disorders (Chapter 3) as intricate results of interaction between genetic and environmental factors. In the following six chapters pathological conditions controlled by heredity are discussed, system by system: Eye and ear abnormalities, Abnormalities of the skin, Skeletal and muscular abnormalities, Diatheses and susceptibilities, Diseases of the blood, and Cancer. In each of these chapters the descriptions of symptoms of different pathological conditions are accompanied by suggestions of the possible practical applications (diagnosis, preventive measures, advice on prospective marriages and pregnancies, etc.). The concluding chapter, The future development of medical genetics, deals mainly with the importance of further studies of linkage in man.

The book is well illustrated. The bibliography is too short for a book which undoubtedly will incite many readers to widen their knowledge by looking into the original papers mentioned in the text.



GENERAL BIOLOGY

THE FOUNDATIONS OF CONSERVATION EDUCATION
Education in Conservation. Pamphlet No. 3.

By the Committee on Conservation Education. National Wildlife Federation. Washington, D. C. 60 cents (paper); \$1.00 (cloth). 7½ x 4½; vi + 242; 1941.

This book is extremely timely. While most of those nations which we formerly called civilized are striving to outdo each other in the rush to immolate themselves irrevocably in the insane holocaust, there yet remains a sober-minded "remnant in Israel" who dare to discuss conservation—the preservation of those values whose destruction is one of the aims of modern warfare.

The book consists of a foreword and six essays—perhaps it would be more appropriate to call them sermons, for they all have a pedagogical and a scriptural flavor. One frequently meets the inevitable text about making the desert blossom as the rose, but the reader is reminded that even a blossoming desert is not necessarily an unmixed blessing, if the blossoms are evoked by artificial irrigation. To obtain water for irrigation dams must be built, which may involve the flooding of valuable forest land, or the obliteration of spawning ground of food fish. It is not enough to urge

conservation; the indispensability of intelligent oversight must be stressed, for conservation, like liberty and charity, has had multitudinous sins committed in its name.

A more significant text which one contributor leans upon heavily, is the description of the promised land into which Moses was permitted to look from the summit of Mt. Nebo, which was flowing with milk, honey, and olive oil, which had fountains in its valleys, and whose every occupant had his own vine and fig tree. But when Jeremiah saw the same land a few centuries later, its springs were dried up, its cedars fallen, its herds scattered, and its cities devastated—the result of uncontrolled erosion and heedless exploitation of its resources.

It must be conceded of course, that between the day of Moses and that of Jeremiah the Hebrews had indulged in a long series of exhaustive wars, during which they and their enemies took turns pushing each other backward and forward from Dan to Beersheba. But the isolation of Judaea cannot be charged to war alone. The fact is that war and devastation of natural resources go hand in hand. As one contributor to this symposium expresses it: "Never do men exploit natural resources so recklessly as when they are fighting or preparing to fight if necessary. Of all human activities warfare is the most wasteful of materials snatched from the earth as well as most wasteful of lives. The short-run wastage rises to its maximum and the long-run depletion goes unheeded." It is not owing to any hyper-fertility of its soil that Lancaster county owes its position as the richest agricultural community in the union, but the fact that its population is descended from industrious ancestors who settled in Pennsylvania to escape compulsory military service in the old country.

Of course the compilation of this book was not undertaken in order to disseminate peace propaganda. The authors are simply not blind to the facts, as another quotation indicates:

Whether we set out to destroy predatory animals and end by injuring other living resources which contribute an important part of our food supply, or whether presently we set out by force to destroy the enemies of democracy and end by ensnaring ourselves in dictatorship at home, the effect is the same. We have in either case failed by neglecting to think through to the ultimate result and instead we have submitted to an emotional appeal such as so often dulls the logic of any situation and leads to making ourselves and our children the eventual victims.



ANNUAL REPORT OF THE BOARD OF REGENTS OF THE SMITHSONIAN INSTITUTION *Showing the Operations, Expenditures, and Condition of the Institution for the Year Ended June 30, 1940. Publication 3606.*

Smithsonian Institution. U. S. Government Printing Office, Washington. \$1.50. 9½ x 5½; xiii + 512 + 107 plates; 1941.

As is customary, this report includes, besides the report of the Secretary on the expenditures of the Institution and its projects, a group of papers on timely subjects. The general reader is more or less familiar with most of these subjects through magazine and newspaper accounts, but such accounts are frequently "rewrites" by persons without a scientific background. Within the present report will be found a group of extremely interesting, authentic discussions in the field of science, mainly biological, prepared by outstanding investigators and students. In a limited space we can only list a few of these: Solar prominences in motion; The national standards of measurements; The search for oil; Animal behavior; The national wildlife refuge program of the Fish and Wildlife Service; A living fossil; Insects and the spread of plant diseases; The Mexican bean beetle; Plant-tissue cultures; Prehistoric culture waves from Asia to America; Masked medicine societies of the Iroquois; The beginnings of civilization in eastern Asia; Stonehenge—Today and yesterday; The botany and history of *Zizania aquatica* L. (wild rice).



OBSERVATIONS ON PLANTS AND INSECTS IN NORTH-WESTERN BAJA CALIFORNIA, MEXICO, WITH DESCRIPTIONS OF NEW BEES. *Transactions of the San Diego Society of Natural History*, Vol. 9, No. 31.

By T. D. A. Cockerell. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 12; 1941 (paper).



HUMAN BIOLOGY

THE DOCTORS MAYO.

By Helen Clapesattle. *University of Minnesota Press, Minneapolis.* \$3.75. 9 x 6; xiv + 822; 1941. This voluminous record of the lives and works of the sturdy Doctor W. W. Mayo and his two brilliant sons, Doctors William J. and Charles H. Mayo, in a frontier community is an important contribution to contemporary American history. From both professional and sociological standpoints, William J. and Charles H. Mayo were men of epiphenominal characteristics who exerted a profound influence upon their times.

Entering into general practice with their father in a small western town, after such inadequate laboratory and clinical training as even the better medical schools in the eighteen-eighties afforded, before the importance of antisepsis was generally recognized and modern asepsis was even conceived of, they soon became absorbed in general surgery. This embraced the application of mechanical measures to the relief and cure of affections of any and all of the accessible organs of the body, including eye, ear, nose, and throat.

As their practice expanded in volume and variety and their means allowed, taking turns, they attended first

the clinics of leading surgeons of Chicago, New York, Philadelphia, Baltimore, Boston, and later of Europe. Thus, garnering knowledge in the methods of diagnosis and treatment from many sources to add to the lessons drawn from their own experience, they were the pupils of no one master. Early in their career they attended meetings of medical societies, where, with becoming modesty, they presented their results, often to the astonishment of their colleagues. Combining a judicious blend of boldness in attack and brilliancy in execution with that uncanny appreciation of each patient's actual physical and psychological state which ever distinguishes the great physician or surgeon, they advanced rapidly to a position perhaps unique among the world's greatest practical surgeons.

The hosts of patients from near and far furnished an experience from which in many fields of surgery they were warranted in speaking with an authority well nigh *ex cathedra*.

Lack of space forbids the tracing of the importance of the Mayo connection with the Mercy Hospital under the capable direction of the Sisters of St. Francis, who supplied Sister Josephine as first assistant to the surgeons at operations, as well as efficient nursing service; the expansion of the hospital to meet the rapidly growing clientele; the gradual addition of talented colleagues to the Mayo partnership, with the establishment of one laboratory and clinical section after another; and finally the development of the great Mayo Clinic and the transfer of its rich holdings during the lifetime of the two brothers to a permanent Trust, the income of which, under the supervision of the State University, is devoted to the advanced training of physicians and surgeons.

Throughout the book, perhaps as its most interesting feature, runs as the *leitmotif* the picture of the mutual love and devotion of the two brothers Mayo ("by my brother and I"), of equal but diverse talents, earnest, honest, direct, generous, and simple in their lives and dealings, who so completely complemented and supplemented each other and whose heads were never turned by the adulation of patients or by the honors accorded them by the profession and institutions.

The book, which is abundantly illustrated with photographs, is prolix in places and, to the general reader, overburdened with local color.



MAYA INDIANS OF YUCATAN.

By Morris Steggerda. *Carnegie Institution of Washington, Publication 531, Washington, D. C.* \$2.00 (cloth); \$1.50 (paper). 9½ x 6½; xx + 280 + 35 figures + 32 plates; 1941.

In this volume Steggerda has brought together much interesting material on the present day Maya Indians. The highly organized society which we know once existed in Yucatan Steggerda believes occurred "when

small migrations of men with new ideas inspired them to build a glorious empire. These men were able to exert their influence only for a limited time, after which their descendants became absorbed into the general population. . . ." The material is organized under the following headings: Piste [where the work was largely done]—past and present; Personality traits and everyday activities; Maize production and animal husbandry; Physical and physiological features; Demography and family history studies.

The outstanding personal characteristics of the modern Maya Steggerda finds to be calmness and cleanliness. Farming provides practically their only means of support. While their ancestors were well advanced in mathematics, astronomy, and architecture the modern Maya have "only numerous strange beliefs, and superstitions concerning the celestial bodies, the winds, the trees, and the ancient ruins."

Numerous records on the physical characteristics, including physical anthropometry of children are given; also the demography of several Indian towns. One of the striking features of the Maya is their excellent teeth—this in spite of the fact that their diet is 80–85 per cent pure carbohydrate and that there is almost no mouth prophylaxis. Another characteristic is the high metabolism, which the author finds must in large part be considered "indication of a real racial effect." The Maya resemble the Chinese in an important, environmentally unaffected character, namely, the configurations of the ridges on the palm." Growth rhythms of the Maya are identical with those of three other races (white, Negro, and Navajo children) selected for comparison. The Maya children and adults are shorter in all ages than are those of the other three races. There are striking physiological similarities in the growth patterns of all four races, in spite of an entirely dissimilar body build and widely different food habits and climatic surroundings. For 605 Maya on whom both birth and death records were obtained, 68.76 per cent died before they were five years old, and 7.93 per cent died between the ages of five and fifteen.

Many graphs and tables and 32 plates are included in this volume, but by far the larger part of the records is in six appendices which are on file at the Division of Historical Research of the Institute.



MARRIED LIFE IN AN AFRICAN TRIBE.

By I. Schapera. *With an Introduction by Bronislaw Malinowski.* Sheridan House, New York. \$3.50. 9½ x 6½; xvii + 357; 1941.

A description of the family life of the Kgatala, a southern Bantu people now living in Bechuanaland, and its evolution during the last century forms the substance of this excellent work. Before contact with the whites (Dutch first and then the English) the Kgatala family constituted the primary unit of domestic living, and in

it were centered the major cultural activities of the tribe. It was the nucleus of the legal, administrative, religious, educational, and economic systems of the tribe, and of course, the mainstay of the sex ethics of the group. With the advent of the laws and religion of the whites, the chief lost his authority, polygamy was abolished and the initiation rites and marriage mores were altered. Furthermore, the men of the tribe were given the opportunity, and were also forced by economic necessity, to obtain wage-paying work away from the village; at the same time the women were enabled to acquire paying skills and training outside the home and the agricultural compound. The effects of such transformations of customs on a population to whom reproduction is the most important obligation can easily be perceived and is revealed in this book with verve, uncommon frankness, and in some detail. Pre-marital and extra-marital sexual unions are now openly tolerated, parental authority has declined considerably, and the family organization has lost its stability. Thus, one sees the usual consequences of the contacts between conflicting civilizations, contacts which produce at least a transitory period in which the system of ethics, the family and social organizations of both civilizations, break down.

The author, preoccupied by the present status of the group he has surveyed, is apparently not aware of the general significance of the phenomenon observed, nor is Malinowski who, in his very laudatory introduction to this work, somehow wishes to tie in the political philosophy of Russia and Germany with the disintegration of the family. Malinowski fails to recall that the demographers of Sweden today present a picture of family life in that country almost identical with that described by the author for the Kgatala.

The author has written this book for the general reader and certainly has succeeded in making it enjoyable as well as instructive. Most of all, Schapera demonstrates a warm sympathy and a remarkable insight into the way of living of the Kgatala whom he has apparently come to know and to thoroughly understand.



SMOKE FROM THEIR FIRES. *The Life of a Kwakiutl Chief.*

By Clellan S. Ford. Yale University Press, New Haven; Oxford University Press, London. \$3.00. 9 x 6; xiii + 248; 1941.

The Kwakiutl once formed a powerful Indian nation, living on Vancouver Island. This is the life story of one of their chiefs, seventy-year-old Charley. The author has recorded Charley's own narrative and through skilful, patient questioning has assembled an unusually comprehensive picture of native customs, as they existed on this island before white contact had altered or eradicated them. The games of the young

children helped to equip them for the life which their culture demanded of them as adults.

... the old men would say to go and get long spruce twigs, and then we go to war with these. Hardly anybody could stand this game. We would whip each other. Anybody who could stand against that was brave. They cut right into your skin, and all of us was bleeding.

When I was quite a big boy, a chief of our tribe called all the chiefs of the Fort Ruperts and told them he was going to give a *tsitsika*. The winter ceremonial is called *tsitsika*, which means "everything is not real." At the Kweka chief's house [during this *tsitsika*], I did my dance—the Warrior dance. I had spruce twigs thrust through the flesh on my thighs by one of the men. He first put a sharp iron through. Then when they took the iron out he put the twig through and put a knot in the twig to hold it together, and the same way in two places on my back. That hurt a little bit, and then they tied a rope onto the twigs and tied it onto the frame of a double-headed snake mask. And they have three poles and lift me up by lifting the mask, and the ropes lifted me and take me along the beach toward the Kweka chief's house. . . . When I am lowered down, they take off the frame and the rope is held by several men, and they begin to pull while I am dancing while they sing my song. . . . And then they begin to pull the ropes and try to break the twigs out of my leg and back. . . . When they couldn't break my skin, they took my knife away from me and cut my skin, . . . Hanging around tied with white thread and a needle stuck in me all over, holding each one of these little paddles, holding a double-headed snake made out of yellow cedar wood in my hands all carved and I come out and dance. That's all I have on when I dance that night. Hemlock branches is around my head.

The old man's frank and detailed account of his life forms interesting reading and represents a very valuable ethnographic document. There is no index.



SOUTHWESTERN ARCHAEOLOGY.

By John C. McGregor. John Wiley and Sons, New York: Chapman and Hall, London. \$5.00. 10 x 6½; x + 403; 1941.

The science of archaeology is as yet too young to be very well systematized. The archaeologists are too busy assembling new material to cooperate in the integration of what is already known. This is as it should be, for no science suffers so much from the advances of so-called civilization as this, with the wholesale destruction of archaeological material when virgin cover is ploughed for cultivation or when ancient ruins are raided to supply modern building material. And what price would be too great to pay for some of the documents destroyed wilfully in the configurations of Alexandria and Tenochtitlan!

But the time when archaeology shall be integrated into a systematic science is no longer remote. The present work seeks to accomplish that task for that portion of the United States where archaeological remains are the most numerous. Not only was the

population density in the southwest higher than elsewhere on the continent in prehistoric times, but exactly the opposite condition obtains today, so that the artifacts of early cultures have been but little disturbed.

The book begins with a description of the geology, physiography, and climatic conditions of the area, then follows a discussion of the historic record, the method of dating ruins by dendrochronology, a discussion of the different routes by which man came to the Western Hemisphere, and a discussion of the sources of information. All of this is purely introductory material. Then follows the main portion of the book—a description of the arrow points, pottery, and refuse and burial mounds that have been dated, together with numerous excellent photographs of many of them. These are presented not as so many isolated facts, but are tied into each other so that they constitute a related whole.

At the end of the book are several appendices containing lists of archaeological sites, dates of different types of pottery, etc., and a glossary of technical terms, with detailed bibliography and an extensive index.

We need more archaeological works of this sort.



THE HAWAIIAN PLANTER. Volume I. *His Plants, Methods and Areas of Cultivation*. Bernice P. Bishop Museum Bulletin 161, 1940.

By E. S. Craighill Handy. The Bernice P. Bishop Museum, Honolulu. \$2.50. 10 x 6½; iii + 227 + 8 plates; 1940 (paper).

The author holds the opinion that subsistence agriculture of native peoples should become the object of study by ethnologists. This aspect of material culture is of prime importance and is also less changeable than many of the arts and crafts which have mainly occupied the attention of ethnologists in the past. The volume deals with the cultivated plants and the agricultural technics of the Hawaiian before he came in contact with Westerners. One of the difficult phases of this work has been the translation of the rich Hawaiian vocabulary dealing with plants and their various parts into scientifically accurate English.

More than half of the book is devoted to the study of taro: the methods of planting both wet and dry taro, its uses, and the planting districts on the various islands. In Hawaii, where hundreds of varieties of such cultivated plants as taro exist, the ethnologist faces the problem of the complicated taxonomy of the subsistence crops with which he is concerned. The author has endeavored to meet this in his extensive research in the field. Very detailed lists of Hawaiian names for varieties, especially of taro and sweet potatoes, are given. How far this material can be successfully applied in further studies is difficult to judge. At least the book brings out interesting points regarding the multitude of uses to which a single plant has been put and the remarkably large number of varieties which

have been developed for use in restricted localities with differing soil and climatic conditions.

Sweet potatoes, yams, bananas, sugar cane, bread-fruit, coconut and a number of less-known Hawaiian food plants account for the rest of the book. It is well illustrated with drawings intended to help students to identify varieties of the main early food plants of Hawaii, with maps showing planting localities, and with photos of plants and fields under cultivation.

This book will especially interest the student of anthropology and all those concerned with elements of material culture of the early Hawaiians and of Polynesians in general.



THE SOCIAL LIFE OF PRIMITIVE MAN.

By Sylvester A. Sieber and Frans H. Mueller. B. Herder Book Company, St. Louis and London. \$3.50. 8 x 5½; xiii + 566; 1941.

This volume epitomizes, with some revisions, the well-known *Volker und Kulturen* by Schmidt and Koppers. It outlines the fundamental concepts of the Culture Historical School of Ethnology, a school of thought that holds views which are in many respects sharply in contrast with the prevailing opinion of the majority of ethnologists of this country, at least. The culture historical method seeks to determine the sequence of prehistoric cultures by assuming that this order can be ascertained from the study of existing peoples of various degrees of civilization. That is, the more primitive cultures of the present day represent the survival of more or less universal civilizations that have disappeared. According to this school, three main culture groups preceded the historic civilization. The first in order of antiquity is called "primitive" and is exemplified by the Pygmies, among others. The second, called "primary," is further subdivided into (a) the exogamous totemist culture of higher hunting (Kwakiutl), (b) the exogamous matrilineal culture of horticulturists (Iroquois), (c) the exogamous patriarchal culture of pastoral nomads (Lapps). The third group, termed "secondary," is subdivided into (a) the free patriarchal culture (Battack of Lumatra), (b) the mother right and totemist culture (Dravidics), and finally (c) the free patriarchal culture from which our historic civilization is descended.

The socio-economic characteristics and the presumed development of each of these culture groups are described briefly. Among the main controversial points which derive from this view one concerns the development of the bilateral family which Schmidt believes was present in the primitive cultures, and another is the religious significance of totemism which, according to Schmidt, is over-rated. There are obviously criticisms of a logical as well as a factual nature to be leveled at the method and results. However, it must be admitted that to some degree Schmidt has achieved a broader

synthesis of the subject than has so far been possible heretofore.



CRIMINOLOGY. *A Scientific Study of the Modern Crime Problem.*

By Eligius Weir. Introduction by Father Flanagan. Institute for the Scientific Study of Crime, Joliet, Illinois. \$3.00. 9 x 6; xx + 329; 1941.

Father Weir has for a number of years been chaplain in the Illinois Penitentiaries of Joliet and Stateville, and at the same time is Professor of Criminology at the College of St. Francis. The combination of these several attributes has led to the viewpoint which emphasizes the responsibility of society with regard to both the prevention of crime and the reformation of the criminal. In this volume which is proposed as a textbook he presents a comprehensive survey of (1) the criminal laws of this country, (2) crime detection and law enforcement agencies, (3) the functions of the legal profession, (4) prison systems and punishment of crime. His discussion of these topics is highly critical. He points out the inconsistencies of the laws in relation to the punishment of crimes, the official complacency towards misdeeds by the legal profession and the flaws in the practical management of the problems of imprisonment and of probation. In brief, he puts his finger on the very weaknesses which from time to time are glimpsed but never wholly perceived by the general public. He cites case after case to bring home his points, and if names and places had been included either the author would himself be placed in prison or else the public would be aroused to violence. Father Weir offers many constructive suggestions to remedy the evils. Among these are the standardization of criminal laws throughout the country, the removal of politics from the judiciary, the centralization of law enforcement agencies, the recognition of the relation between crime and physical and mental disorders, the development of more adequate methods of meting punishment to take into account the personality of the criminal and the possibility of his reeducation. The author believes also that crime can be prevented through the efforts of the church, the home, and the school. This is a well-written book and one to interest all citizens in all professions.



FAMILY EXPENDITURES FOR CLOTHING. *Five Regions. U. S. Department of Agriculture Miscellaneous Publication No. 428. Consumer Purchases Study. Farm Series.*

By Day Monroe, Maryland Y. Pennell, Elizabeth Phelps, June C. Hopper, and Helen Hollingsworth. Government Printing Office, Washington, D. C. 30 cents. 9½ x 5½; iv + 387; 1941 (paper).

FAMILY EXPENDITURES FOR FURNISHINGS AND EQUIPMENT: Five Regions. *U. S. Department of Agriculture Miscellaneous Publication No. 436. Consumer Purchases Study. Urban, Village and Farm Series.*

By Day Monroe, Helen Hollingsworth, Margaret Perry, and Maryland Y. Pennell. Government Printing Office, Washington, D. C. 25 cents. 9½ x 5½; iv + 212; 1941 (paper).

The first of these reports, on ways of spending for clothing, is a study of

non-relief, unbroken, native-white families of farm operators in 13 farming sections representing the major types of agricultural production in this country. Farm laborers and paid managers were excluded except in the Southeast where a special study was made of the tenure-labor group, sharecroppers. Data for Negro families, both operators and sharecroppers, were also obtained in the Southeast region and are presented separately.

Groups of counties in the general farming section of Pennsylvania and Ohio were selected for special text presentation, and more detailed discussions on the use of clothing funds by each of 11 groups of family members are furnished for a large analysis unit that combines all the farm communities surveyed in the North and West.

The second report dealing with expenditures for household furnishings and equipment is based on surveys made on families living in 13 farm sections, 140 villages, and 20 small cities—data for Negro families, for the Southeast region only, being presented separately.

As in all previous reports on the Consumer Purchase Study (conducted under the auspices of the Works Projects Administration) statistical tables form a large part of the surveys.



ABOUT OURSELVES. A Survey of Human Nature from the Zoological Viewpoint.

By James G. Needham. *The Jaques Cattell Press, Lancaster, Penna.* \$3.00. 10 x 6½; xi + 276; 1941.

Popular books on man from the point of view of naturalists are always needed, lest man forget that he is merely one of nature's endless experiments and as such is governed by inescapable biological laws which can explain (and excuse) his makeup and behavior with all its imperfections and compromises. Professor Needham has produced an outstanding volume of this sort by writing in an attractive, clear style, by presenting well-chosen chapters without unessential detail, and by consistently avoiding proposals and propaganda for improving mankind. The author's blunt and self-assured philosophy permeates his writing in a fashion stimulating to the layman and challenging to the specialist. He never hesitates to explain the most puzzling problems in often original, though at times all-too simplified, a manner. At various places his

arguments carry the discussion far from the proper domain of biology and appear somewhat naive.

The first 71 pages furnish a biological background with condensed surveys of the animal kingdom, the order of primates, fossil men, and the development of the brain. The subsequent 200 pages deal chiefly with some biological aspects of really psychological and sociological subjects and include such topics as religion, folkways, government, and war. Concerning war, the most timely of these varied items, it is stated that "ours is a fighting species." In such species the males are larger than the females, they are better armed, more gaudily decorated, more highly endowed vocally, and are willing to defend the family. One wonders whether even lay-readers can be convinced by these and many similar, sweeping generalizations.



DEEP SOUTH. A Social Anthropological Study of Caste and Class.

By Allison Davis, Burleigh B. Gardner and Mary R. Gardner. *The University of Chicago Press, Chicago.* \$4.50. 7½ x 5½; xv + 558; 1941.

Following the pattern already set by a number of investigators, the authors, assisted by other field workers, lived for two years in a southern town, "Old City," and there participated in the social life of the community to study the socio-economic stratifications of the whites and of the Negroes, and the interactions between the two color groups. Their observations are reported in detail and in summary indicate that the inhabitants of the community

live in a social world clearly divided into two ranks, the white caste and the Negro caste. These color-castes share disproportionately in the privileges and obligations of labor, school and government, and participate in separate families, associations, cliques, and churches. Only in the economic sphere do the caste sanctions relax, and then but for a few persons and in limited relationships. Within the castes are social classes, not so rigidly defined as the castes, but serving to organize individuals and groups upon the basis of 'higher' and 'lower' status, and thus to restrict intimate social access.

Such findings would have been expected, but, although the wealth of information acquired has importance, one is struck by the superficiality of this kind of survey. There is obvious need for precise data on social behavior in our civilization but it seems that, since already a certain fund of knowledge is at hand, students of the subject could and should attempt to probe deeper into the matter. However, this excellent piece of accurate reporting is not to be dismissed as inconsequential since it again brings to the fore one of the most important problems that faces the country, to wit, the problem of stabilizing the relationship between the whites and Negroes.

BECOMING A KWOMA. *Teaching and Learning in a New Guinea Tribe.*

By John J. W. Whiting. With a Foreword by John Dollard. Yale University Press. \$2.75. 9 x 6; xix + 226; 1941.

Anthropology has barely begun to study intensively the problems concerned with the transmission of culture or group habits from one human generation to the next. Such study must deal with child training, the processes of teaching and learning, as influenced by reward and punishment, and the causes of the origin or disappearance of cultural traits. The ultimate and generally valid conclusions from research of this nature will have to rest upon many comparative observations, gathered laboriously among widely differing tribes and cultural levels.

The present scholarly, yet very readable contribution, is the result of field work in a primitive, homogeneous, and economically non-specialized tribe (Kwoma) from the interior of New Guinea, north of the Sepik river. The first part is largely descriptive, picturing the varied aspects of Kwoma culture, particularly as they affect the daily life of children from infancy to adulthood. The second part deals extensively with theories of learning and of socialization in a careful attempt to analyze the behavior of these Kwoma children in the course of their development. In this, the author leans heavily upon Freudian hypotheses, paying much and quite uncensored attention to the rôle of sex.

From some passages in the book it appears that these naked savages can teach their offspring to behave properly with more ease, grace, and effect than is at the command of many a civilized parent.

There is a useful index, but there are only a few and mediocre illustrations.



YALE UNIVERSITY PUBLICATIONS IN ANTHROPOLOGY. Numbers 23 and 24. *Excavations in the Ft. Liberté Region, Haiti*, by Froelich G. Rainey; *Culture of the Ft. Liberté Region, Haiti*, by Irving Rouse.

Yale University Press, New Haven; Oxford University Press, London. Nos. 23 and 24 bound under one cover, and sold only as a unit, \$3.50. 9½ x 7; No. 23, 48; No. 24, 181 + 35 plates; 1941 (paper).

The first half of this study is largely a description of the field work relating to the archeological investigations conducted by the Yale Peabody Museum in the Ft. Liberté Bay region of northern Haiti in the summers of 1934-35. In all, eleven different sites in this region were excavated with the help of native guides and workers. The discussions include detailed descriptions of the methods of locating worthwhile sites, the geological stratification of each, and the skeletal finds.

The second part of the study is concerned with a description and classification of the cultural artifacts

collected during the investigation. Included in this report also are discussions relating to the probable modes of subsistence, social organization, language, religion, burial, trade, and warfare of the now extinct native Indian population of Haiti. From the data at hand, it is evident that the native Indians of Haiti were similar in many respects to their contemporaries in Central and South America, and had reached a fairly high point in their neolithic culture.

Both reports are well documented, and present an abundance of tabular and illustrative material in support of the discussions. Each carries a table of contents.



AN APACHE LIFE-WAY: The Economic, Social, and Religious Institutions of the Chiricahua Indians.

By Morris Edward Opler. The University of Chicago Press, Chicago. \$5.00. 8 x 5½; xvii + 500; 1941.

The exposition of the subject particularly distinguishes this ethnographic description of the Chiricahua Apache. The author seeks to portray in order the sequence of social reactions manifest by these Indians from birth to death. One by one he introduces the societal elements: family, culture, economy, religion, etc. which affect the life of the individual and mold him into an Apache. This approach is very effective and is rendered even more interesting by the abundant use of direct quotations from the Indian informants. Hence, the present work acquires almost the characteristics of an autobiography of a composite Chiricahua, and the personality of the author seemingly intrudes very little. By such a method the rationale of the individual or group reactions is clearly brought out and is not the product of the inferences of the observer from another civilization. By the same token one also runs the risk that the informant will seek to justify the actions of his group in terms of the observer's social values. Thus, in the text one notes that the informants emphasize continuously the peacefulness, morality, and other Christian virtues of the Chiricahua. If these are flaws they are the only ones to be noted in this thorough and authoritative account of the life and mores of the Apache group studied.



DIE VIERLINGSGESCHWISTER GEHRI UND IHR VERWANDTSCHAFTSKREIS. Eine familienanthropologische Untersuchung. Archiv der Julius Klaus-Stiftung, Band 15, Heft 1.

By Otto Schlaginhaufen. Art. Institut Orell Füssli A.-G., Zürich. 9½ x 6½; 309-398 + 10 genealogical tables + 7 plates. 1940 (paper).

The subjects of this study—Oskar, Bertha, Rosa and Arthur Gehri—were born as four-ovum quadruplets in Switzerland in 1880 and were still living and in good

health at the time this monograph was written. The most complete anthropometric data were obtained by the author when they were 45½ years of age. Data on the earlier years of their life were obtained from various sources, including hear-say information and studies of photographs. In infancy and early childhood they looked alike and their personalities were similar. Differences became more apparent as they grew older but even in middle age they were more similar to each other than to any of their 3 single sibs and 3 half-sibs, and also more similar than were any other individuals of their sibship to each other. The author ventures the hypothesis that environment may here have played a rôle, as their environment in successive years was more similar at a given age than that of the other sibs born several years apart. Pedigrees of the maternal and paternal direct and collateral lines for five generations were also studied. The families of both parents showed a history of twinning. That of the mother had 7 pairs of twins in the paternal and 5 pairs in the maternal lines. The father's mother was a twin and one of his nieces bore a twin. The pedigree charts are appended and there is a bibliography.



KÖRPERLICHE ENTWICKLUNG NACH FORM UND LEISTUNG BEI MITTELSCHÜLERN VON AARAU.

By *Eugen Morf*. *Manatschal Ebner and Cie, Zurich*. 9½ x 6½; 231 + 29 tables; 1939 (paper).

The greater portion of this book is devoted to the absolute and relative figures found in a large series of anthropological measurements made on 477 boys and 170 girls between the ages of 16 and 20 in Aarau, Switzerland. In addition to body measurements, measure of pulling capacity, hand grip strength, running high jump and running broad jump, exercises on horizontal bars, climbing, and weight pulling are included. It was noted that growth continued in practically all height and breadth components in both girls and boys from the ages of 16 and 19 years. The exceptions were ilio-spinal height, tibial height, and hand breadth and length. Growth was more evident in boys than in girls beyond the age of 16. In the same sample studied, groups from the upper social classes tended to be both taller and heavier than the boys and girls from the lower income brackets. An appendix tabulates the statistical means, coefficients, and ranges for each measurement made, grouped by age and sex. There is a bibliography.



WESTERN AND SOUTHWESTERN INDIAN SKULLS. *University of Denver Anthropological Series, First Paper, 1941.*

By *E. B. Renaud*. *University of Denver, Denver*. 85 cents. 8½ x 11; 94; 1941 (paper).

During the past fifteen years Renaud has published in various places records on Indian skulls from the Western Plains and Southwest. He has now brought this material, as well as hitherto unpublished data, together under one cover in order to make it more readily accessible. The material is grouped as follows: Western crania or Plains Indians skulls (Nebraska and Colorado skulls); Southwestern crania (Pueblo, Basket Maker, and Mound Builder skulls); and a Palaeo-American type (comparative study of prehistoric skulls).

The numerous tables of measurements and indices of crania studied which form part of the report are a useful contribution to the literature of physical anthropology of the American Indian. The study concludes with a bibliography of 45 titles.



ZOOLOGY

GUIDE TO THE FISHES OF THE GREAT LAKES AND TRIBUTARY WATERS. *Cranbrook Institute of Science Bulletin No. 18, August, 1941.*

By *Carl L. Hubbs and Karl F. Lagler*. *The Cranbrook Press, Bloomfield Hills, Mich.* \$1.00 (cloth); 50 cents (paper); 9 x 6; [100] + 16 plates; 1941.

The systematic and geographic relationships of some of the forms of the fish fauna of the present Great Lakes and its tributaries "have been rendered very complex by the continental glaciers which covered the region during the Ice Age, as well as by evolution." In the glacial era the large bodies of water which formed in front of the great ice cap overflowed southward to the Gulf through the rivers of the Mississippi valley, and to the Atlantic Slope through the Susquehanna, Mohawk, Hudson, and St. Lawrence valleys. With the retreat of the ice sheet the lakes became smaller and drainage from the southern region of the Great Lakes Basin much restricted. The waters from the Finger Lakes region and from central New York, however, turned into the Lake Ontario basin. In modern times canals have restored the connections of the Great Lakes waters with those of the great rivers to the south, and the barrier of Niagara has been broken down by the Welland and Trent canals. In addition to the early fish fauna of the Great Lakes Basin and the forms which have entered more recently through the artificial connections, the smelt, landlocked salmon, brown trout, rainbow trout, carp, and gold fish have been introduced by stocking.

The present guide lists 229 kinds of fishes, native and introduced, "which are now known to live in the Great Lakes and their tributaries, or to have occurred there in historic times, . . ." Detailed directions for counting scales, fin rays, etc., and for measuring body lengths and other dimensions are given as a basis for learning

the salient characters of fishes. The keys are well planned and, in a group of plates, figures of 118 forms are shown. The geographic range—an excellent map is provided—of species and subspecies has been worked out not only from published material but from a great amount of original data. Much of the original information is based on specimens and records in the University of Michigan Museum of Zoology. The work concludes with a reference list of eight pages and an excellent working index. A guide which will be found extremely useful by the amateur as well as by the professional zoologist.



A MONOGRAPH OF THE EXISTING CRINOIDS. Volume I. *The Comatulids. Part 4a. Superfamily Mariametrida (excepting the family Colobometridae). Smithsonian Institution, U. S. National Museum Bulletin 82.*

By Austin H. Clark. U. S. Government Printing Office, Washington. \$1.50. 12½ x 9½; 603 + 61 plates; 1941 (paper).

Several monographs have already been issued from the U. S. National Museum on the crinoids. Parts 3, 4, and 5 of Volume I, Bulletin 82, include the systematic discussion of the species and higher groups of living comatulids, or unstalked crinoids. Part 3 (cf. Q. R. B., Vol. 7, p. 114), published in 1931, includes the superfamily Comasteridae. The present volume, a continuation of Part 3, includes the account of the second of the three superfamilies of the Oligophreata, with the exception of the Colobometridae. The volume represents an enormous amount of detailed, careful, taxonomic work upon a difficult group. It is illustrated with a group of fine plates (283 figures).

Since the publication of previous work dealing with the structure and morphology of the comatulids was published much additional work has been done by others. Some of these authors have differed with Clark on interpretation of structural peculiarities. In the first 73 pages of the present volume Clark presents a summary of their work. He fails to find, upon a careful analysis, any reasons for altering his opinions already expressed.

The main point of divergence between my opinions and those of my colleagues hinges upon the weight to be given the Paleozoic and earlier Mesozoic forms in an elucidation of the structure of recent types. I maintain that until the recent crinoids are far better known than they are at present, especially in regard to their younger stages, it is futile to attempt to interpret the details of their structure from comparison with earlier forms. For most of the earlier forms, as we know them, represent the terminal twigs of developmental branches of which the generalized beginnings are unknown, just as the adults of the recent forms represent the ultimate product of an unknown ontogeny. And even if the earlier stages of all the recent forms were known, it is by no means certain that these would give any definite clue to their ancestry

and morphological relationships when compared with the adults of earlier types. Until we are in possession of sufficient facts to enable us to understand the recent types, and thus to be sure of our ground, we are likely to be led astray rather than aided by any detailed comparison with fossil types."



SYSTEMATIC CATALOGUE OF THE FISHES OF TORTUGAS, FLORIDA: *With Observations on Color, Habits, and Local Distribution. Papers from Tortugas Laboratory, Volume XXXIV. Carnegie Institution of Washington Publication 535.*

By William H. Longley. Edited and Completed by Samuel F. Hildebrand. Carnegie Institution of Washington, D. C. \$3.50 (cloth); \$2.50 (paper). 10 x 6½; xiii + 331 + 34 plates; 1941.

The late Dr. Longley was a pioneer in using the diving helmet for the study of fishes in their natural environment. He found that many fishes are not afraid of the diver. Thus he was able to approach them and make his observations on behavior, feeding habits, and adaptive coloration at close range. An under-sea camera and a wax-covered slate for taking notes, which were later transcribed to paper, were part of his equipment. Longley was unable to complete the present monograph but at his request, Hildebrand, senior ichthyologist of the U. S. Fish and Wildlife Service, has performed this task. Organizing and bringing to fruition the work of another is always a difficult undertaking, requiring laborious research for a comprehension of the author's notes and records. Hildebrand has done this with skill and understanding. In the Introduction he says:

Without doubt, Dr. Longley, after a quarter of a century of diving at Tortugas and elsewhere, knew the habits and haunts of tropical and subtropical reef fishes better than any other person of his day." . . . the most important part of this monograph consists in the under-water observations reported. These observations are the more important because of Dr. Longley's accurate knowledge of species. It is evident from the great amount of time he spent in museums . . . during the later years of his life in the study of types and other important specimens that he was more and more impressed, as his work progressed, with the supreme importance of the proper recognition of species.

Among the 34 plates at the end of the volume will be found many interesting photographic reproductions showing various forms of fishes in their natural habitat. A complete index of the forms described is provided. Both the systematist and the student of the biology of fishes will find this a valuable reference work.



MOSQUITOES OF THE ETHIOPIAN REGION. III. *Culicine Adults and Pupae.*

By F. W. Edwards. *The British Museum (Natural History), and Oxford University Press, London.* 16s. 10 x 7; viii + 499 + 4 plates. 1941.

Two parts of this valuable reference work have been previously issued. Part I—*Larval Bionomics of Mosquitoes and Taxonomy of Culicine Larvae*, by G. H. E. Hopkins was issued in 1936 (cf. Q. R. B., Vol. 12, p. 109); Part II—*Anophelini: Adults and Early Stages*, by A. M. Evans, in 1938 (cf. Q. R. B., Vol. 14, p. 245). The present volume completes the Monograph. The author's death occurred as the material was about to go to press.

The number of known species of Culicine mosquitoes of the Ethiopian region has advanced from about 180 in 1927 to about 290 now described, besides some 40 named subspecies and varieties. This increase "is in part due to the rectification of errors through which forms which are now considered distinct species had been lumped together, but still more to the discovery of numerous forms which until recently were entirely unknown." Although the author had a vast amount of material at hand "much further collecting is needed before the African fauna can be catalogued upon a basis that is secure both as to specific limits and generic conceptions." The information herein given is sufficient, however, to identify all but a few of the African mosquitoes with certainty. Included in the description of each species is information on distribution, so far as now known—but this data, it is stated, is often far from complete.

In Section IV.—Zoogeography of Ethiopian Mosquitoes, the following topics are discussed: (1) Comparison with mosquito faunas of adjacent regions; (2) Faunal divisions of Africa as exemplified by mosquitoes; (3) Ecological classification; (4) Present distribution in relation to the past; (5) Sources and extent of our present knowledge; (6) List of Ethiopian mosquitoes with summarized distribution. Numerous illustrations are given in the text, a list of references is provided also an index to the names of mosquitoes.



TOTO AND I: *A Gorilla in the Family.*

By A. Maria Hoyt. Introduction by Roger Conant. J. B. Lippincott Company, Philadelphia and New York. \$2.50. 8½ x 5½; xxiv + 238; 1941.

This is a popular account of the daily happenings in the life of that much publicized anthropoid debutante "Toto," now the bride of the famous gorilla "Gargantua." The late Mr. Hoyt shot Toto's father in French Equatorial Africa and Mrs. Hoyt adopted the helpless infant, for which a native wet-nurse had to be found. Toto lived in a luxurious home under devoted care for nine years when her 438 pounds became too large a problem and she had to start a public career in a circus. This happened after she had carried a Japanese servant up into a tree.

In view of the sudden and unpredictable changes in the temper of adolescent apes one reads with shudders of the freedom Mrs. Hoyt had granted to her house pet and "problem child" long after such indulgence had ceased to be a reasonable risk. In one of the last chapters, entitled "Toto the Comforter," the author admits that:

Our difficulties were always tremendously increased during two or three days of every month when Toto seemed to fall in love with one of the men. Sometimes it was one of the gardeners, a tall handsome chap, sometimes José, the second chauffeur, sometimes the butler. During these periods, she would follow the object of her affections about the grounds, . . .

The primatologist will welcome the 35 good photographs illustrating the rapid development of a gorilla, but he will be disappointed to find no sound observations of scientific value for which existed such rare opportunities. To judge by her extraordinary weight and by her most recent pictures Toto has developed into the equivalent of a professional Fat Lady and it seems doubtful that her coming wedded life will result in a blessed event. Let us hope this prognosis is wrong and that Toto will soon present Gargantua and what is left of the scientific world with the first captive-born gorilla!



A LOT OF INSECTS. *Entomology in a Suburban Garden.* By Frank E. Lutz. G. P. Putnam's Sons, New York. \$3.00. 8½ x 5½; 304; 1941.

Rarely do we find a book whose title so nearly embodies the essence of the subject matter as is the case of *A Lot of Insects*. Within these pages the author has recorded in a very interesting manner, his experiences of the past several years in observing, collecting, and experimenting with the "six-footed visitors" which have come to his suburban garden. The astounding feature of the work is that on a lot measuring 200 x 75 feet, the author has casually collected and identified no less than 1402 separate species of insects. The collected materials now make up a feature attraction labelled "Insects of a Suburban Yard" in the display room at the American Museum of Natural History.

The subject has been presented in a very unique and unorthodox fashion, following neither taxonomic nor pedagogic principles, but just in the order in which the author remembered the experiences. The text is rich in experimental observations, particularly with respect to the insect's special senses, habits, and sounds. The clarity with which the author has stated his experiences is surpassed only by the frankness with which he admits that there is much yet to be learned about the ways of insects.

The frequent excursions from the purely scientific to the humorous and imaginative phases of entomology make for delightful and stimulating reading. Through-

out the work there is mild plea for a better popular understanding of insects both from the point of view of their charm and interest *per se*, as well as from the aspect of their economic importance. The footnotes are gathered into a 42-page "In Addition" at the end of the volume. The text is supplied with an abundance of excellent illustrative material and an index.



FACTORS AFFECTING THE GENERAL STATUS OF WILD GEESSE AND WILD DUCK. *International Wildfowl Inquiry, Volume I. The International Committee for Bird Preservation (British Section).*

By Various Authors. With a Foreword by Percy R. Lowe. Cambridge University Press, Cambridge; The Macmillan Company, New York. \$2.25. 9 $\frac{1}{2}$ x 6 $\frac{1}{2}$; x + 123; 1941.

In less than a hundred years there has been a complete revolution in the conditions governing the habits and numbers of wildfowl in many parts of the world. The breech-loading gun, the steam-engine, the motor car, and motor boat, to mention only a few examples, have not only enormously increased destruction, but by disturbance of previously quiet and unmolested breeding grounds in the far north, have led to marked changes in distribution. To obtain both general and specific information concerning this state of affairs, the International Committee for Bird Preservation has adopted a far-reaching program of investigation. This first volume of the Committee's report contains an introduction describing the events leading to the formation of the Wildfowl Inquiry Sub-committee and eight papers by specialists, namely: Conditions in northern breeding areas; The distribution of *Zostera* and other seashore plants in relation to the migration of wildfowl; British decoys; Punt-gunning; Ringing of duck at British decoys; Results of ringing duck; and Close time. Although the report deals with conservation problems in Europe, and the British Isles in particular, American conservationists would do well to acquaint themselves with the information gathered about a problem which is world-wide in scope.



FIELD BOOK OF SNAKES of the United States and Canada.

By Karl P. Schmidt and D. Dwight Davis. G. P. Putnam's Sons, New York. \$3.50. 6 $\frac{1}{2}$ x 4; xiii + 365 + 34 plates; 1941.

Not even fish-stories deviate from the truth as often and as far as do popular beliefs regarding snakes. This splendid little volume is of much-needed help in replacing snakelore with sober herpetological information, authoritative, comprehensive, well arranged, and not overburdened by unessential detail. The first of the many excellent photographs shows a rattlesnake

unhesitatingly crossing the horsehair rope with which a camper had thought to safeguard his sleep.

The great variety of subjects considered in the first part includes the history of the study of North American snakes, an anatomical description of the poison apparatus, the treatment of snake bite, the methods of collecting and preserving snakes, and suggestions to amateur students for new and useful observations on snakes.

The largest part of the volume gives a systematic account of all our snakes with as clear and convenient keys for species determination as this complicated matter permits. A great many text figures, showing head formation, scale pattern and geographical distribution, a selected bibliography, and a lengthy index add to the usefulness of this field book.



THE HERPETOLOGY OF HISPANIOLA. *Smithsonian Institution. United States National Museum Bulletin 177.*

By Doris M. Cochran. U. S. Government Printing Office, Washington, D. C. 70 cents. 9 $\frac{1}{2}$ x 6; vii + 398 + 12 plates; 1941 (paper).

The natural history of island fauna has for many years provided pertinent material for studies in taxonomy and evolution. While the present study of the herpetology of Hispaniola is concerned largely with taxonomy, it is apparent that the extremely rough topography of the island has been responsible for the isolation and subsequent evolution of many interesting forms.

The author's purpose of "advancing the survey of the amphibian and reptile fauna of the Greater Antilles" has been amply fulfilled in this report. The work, based on many years of painstaking field and museum observations, lists 14 families representing 32 genera and numerous species of amphibians and reptiles native to Hispaniola. The discussion of each species includes a detailed description, a list of measurements, the principal variations, the habitat, the paratype, and the relationships to other species. The work is abundantly supplied with tabular material and illustrations, both graphic and photographic. For most of the amphibians, the illustrations include a dorsal and ventral view of the entire body, a profile of the head, an interior view of the mouth, and a view of the under side of the hand and foot. For the reptiles, the illustrations show the scale pattern for the top of the head, the profile, and the chin. The study is documented with a 5-page bibliography, and carries a comprehensive index.



ZOOLOGICA. *Scientific Contributions of the New York Zoological Society. Volume XXVI, Part 3, Numbers 19-27.*

New York Zoological Society. Zoological Park, New York. \$2.00. 10½ x 7; 143 + 28 plates; 1941 (paper).

This number contains the following papers:

Eastern Pacific Expeditions of the New York Zoological Society. XXVI. Crabs of the Genus *Uca* from the West Coast of Central America, by Jocelyn Crane (9 plates, 8 text-figures); Eastern Pacific Expeditions of the New York Zoological Society. XXVII. A Study of Young Sailfish (*Istiophorus*), by William Beebe (5 plates, 9 text-figures); On the Reproduction of *Opsanus beta* Goode & Bean, by Charles M. Breder, Jr. (2 plates); On the Reproductive Behavior of the Sponge Blenny, *Paraclinus marmoratus* (Steindachner), by Charles M. Breder, Jr. (3 plates, 1 text-figure); The Chromatophores of *Fundulus heteroclitus* in Polarized Light, by A. M. Shanes and Ross F. Nigrelli (3 plates); New Races of Alaudidae and Timaliidae from Northern Thailand, by H. G. Deignan; Respiratory Behavior in Fishes not Especially Modified for Breathing Air Under Conditions of Depleted Oxygen, by Charles M. Breder, Jr. (1 plate); Eastern Pacific Expeditions of the New York Zoological Society. XXVIII. Fishes from the Tropical Eastern Pacific. [From Cedros Island, Lower California, South to the Galapagos Islands and Northern Peru.] Pt. 3. Rays, Mantas and Chimaeras, by William Beebe and John Tee-Van (4 plates and 40 text-figures); Erotylidae of Kartabo, Bartica District, British Guiana. (Coleoptera.), by C. H. Curran (1 plate and 1 text-figure).



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY⁹ Vol. 46, No. 1. *The White-Crowned Sparrows (Zonotrichia leucophrys) of the Pacific Seaboard: Environment and Annual Cycle*, by Barbara D. Blanchard.

University of California Press, Berkeley. \$2.00. 10½ x 6½; 135 + 20 plates; 1941 (paper).

The general plan of this study has been to assemble the most complete picture possible of the year-round behavior and reproductive physiology of two populations of white-crowned sparrows, one migratory, the other resident, of widely separated breeding areas. Great emphasis is laid on the history of the male reproductive system as a slow and exquisitely precise time-keeper for individual, racial, and environmental comparisons. Some attention is given to the relatively minor aspects of behavior which are, so to speak, the superficial aspects or indicators of the more deep-seated, cyclic pattern. The book is of particular interest in that it develops the thesis that an understanding, not of minor structural modifications but of the relationship of the annual cycle to the environment, offers the most promising road to the center of problems of distribution and potential evolutionary change.



FROM ROBIN TO JUNCO. *Stories of Birds and What They Do.*

By Mary I. Curtis. Houghton Mifflin Company, Boston. 96 cents. 7½ x 6; 216; 1941.

When city-bred Ann visited her bird-loving uncle in the country he taught her how to observe birds and told her about the habits, characteristic behavior, and foods of many kinds of birds. The descriptions of their rambles and their conversation about the birds they saw—robins, hummingbirds, cardinals, woodpeckers, cowbirds, crows and many others—are reported in this book for the 8 to 11-year olds. The text is written with authority but in a manner to stimulate the interest of the age group for which it is intended. It is printed in a large, clear type which, together with the illustrations, makes a book which should be attractive to children. The illustrations consist of twelve color photographs by Arthur A. Allen of Cornell University and charming black and white drawings on nearly every page which depict characteristic poses and, in many cases, the animation of the birds. The simple, well-planned index is prefaced with explanations for its use by the inexperienced. The end papers show routes of the migratory birds who make their summer homes in the United States east of the Mississippi. The book is suitable for grade-school and public libraries and the child's own book-shelf.



THE BIRDS OF NORTH AND MIDDLE AMERICA: *A Descriptive Catalog of the Higher Groups, Genera, Species, and Subspecies of Birds Known to Occur in North America, from the Arctic Lands to the Isthmus of Panama, the West Indies and Other Islands of the Caribbean Sea, and the Galapagos Archipelago.* Smithsonian Institution, United States National Museum Bulletin 50.

By Robert Ridgway. Continued by Herbert Friedmann. U. S. Government Printing Office, Washington, D. C. 40 cents. 9½ x 6; ix + 254. 1941 (paper).

The ninth part of this well-known descriptive catalog of birds contains the Gruiformes with the families Gruidae (cranes), Rallidae (rails, gallinules, and coots), Heliornithidae (sun-grebes), and Eurypygidae (sun-bitterns). Although the size of the present volume has been reduced from its original bulk to permit more immediate publication, none of the essential data has been omitted by Friedmann.

All descriptions are based upon a thorough study of specimens and the literature; nothing has been accepted merely because it was written. The sequence of orders in the volume continues to follow Ridgway's plan, but the arrangement of families, genera, species, and subspecies within each order is patterned to agree with that given in Peters' *Check List of Birds of the World*.



PELAGIC WHALING IN THE ANTARCTIC. IX. THE SEASON 1938-1939. *Hvalrådets Skrifter, Scientific Results of Marine Biological Research, No. 25.*

By Birger Bergersen and Johan T. Ruud. Jacob Dybwad, Oslo. Kr. 3.50. $10\frac{1}{2} \times 7$; 46 + 2 plates. 1941 (paper).

The statistical data pertinent to the reports of 25 floating factories and 196 catchers that took part in the pelagic whaling of the antarctic during the season of 1938-39 are embodied in this monograph. An abundance of charts and tables are used to indicate the number, size, and sex of the different varieties of whales taken, the amount of oil produced, and the extent of area over which the catchers worked. The data are broken down for the months, and presented in terms of barrels of oil per catcher's day.

An important fact emerging from the data at hand is that of a decrease in the number of large animals taken. This is taken as an indication that the whale stocks of the antarctic are being slowly, but surely depleted.



BIG ZOO.

Described by William Bridges. Photographed by Desider Holisher. The Viking Press, New York. \$2.00. $9\frac{1}{2} \times 6\frac{1}{2}$; 160; 1941.

In this book one of the officials of the New York Zoo relates some of the interesting experiences that have occurred in his career. But the greater part of the work consists of photographs of those things that the general public never sees—chiefly the veterinary hospital.

The book lacks the intimate personal touch of Mrs. Benchley's *Life in a Man-made Jungle*, nor is it as large as that work, which has already become a classic. But the New York Zoo is larger and richer than that at San Diego, and so has a greater variety of animal life on exhibit, and the experiences of its curators are more wide-spread. All told, the authors of this work have succeeded in producing an interesting collection of illustrations, with explanatory text. As it is essentially a narrative, there is no index, nor is there any need for one.



UNDER THE SEA-WIND. *A Naturalist's Picture of Ocean Life.*

By Rachel L. Carson. Illustrations by Howard Freck. Simon and Schuster, New York. \$3.00. $8\frac{1}{2} \times 6$; xix + 316; 1941.

This is a literary interpretation of the animal life of the seashore. While the characters that figure in the story have been imbued with personalities, this has been accomplished with scientific accuracy and is not offensive. The illustrations are well executed and the 41 page glossary very helpful.

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY. Vol. 43, No. 15. *A Study of Oxymonas minor Zetiff from the Termite Kaloterms minor Hagen*, by Joy Barnes Cross. Vol. 47, No. 2. *A Miocene Sea Lion from Lomita, California*, by Gretchen M. Lyon.

University of California Press, Berkeley and Los Angeles. 25 cents each. $10\frac{1}{2} \times 6\frac{1}{2}$; No. 15, 17 + 2 plates; No. 2, 19 + 5 plates; 1942 (paper).

TRANSACTIONS OF THE SAN DIEGO SOCIETY OF NATURAL HISTORY. Vol. 9, Nos. 29, 30, 32, and 33. *The Long-Nosed Snakes of the Genus Rhinocheilus*, by Laurence M. Klauber. *A New Species of Rattlesnake from Venezuela*, by Laurence M. Klauber. *A Vertebrate Faunal Survey of the Organ Pipe Cactus National Monument, Arizona*, by Laurence M. Huey. *Notes on Some Mexican and Californian Birds, with Descriptions of Six Undescribed Races.*

Society of Natural History, San Diego, Calif. $10\frac{1}{2} \times 6\frac{1}{2}$; No. 29, 39 + 2 plates; No. 30, 3; No. 32, 20; No. 33, 7; Nos. 29 and 30, 1941; Nos. 32 and 33, 1942. (Paper.)



BOTANY

AN INTRODUCTION TO THE STUDY OF ALGAE.

By V. J. Chapman. Cambridge: at the University Press; The Macmillan Company, New York. \$3.75. $8\frac{1}{2} \times 5\frac{1}{2}$; x + 387; 1941.

Although intended as a relatively elementary textbook, suitable for university students, this book has a wider usefulness. The first chapter, in the light of more recent taxonomic treatments of the Algae, recognizes and outlines nine living groups and the fossil Nematophyceae. The discussion of these nine groups, covering their morphology, development, reproduction, life histories, distribution, and relationship, occupies the next seven chapters (238 pages). There are numerous helpful illustrations, some from the standard literature, some from less familiar sources, a few original, with many schematic diagrams of phylogeny, relationships, and life histories. While this portion of the book is largely the usual textbook treatment of the field it contains some valuable additional material from the more recent literature and as a whole forms a useful supplement to the well-known texts of Fritsch, Smith, Tilden and others.

It is the second part of the book, however, which greatly extends its value, for in six general chapters, comprising about 130 pages, Chapman presents material not usually made available to the student in phyco-logical texts. His treatment, in Chapter 9, of the general aspects of reproduction and evolution, implemented with schematic diagrams of life cycles and of phylogenetic sequences, with tables of parallelism in evolution, with definitions of significant terms, and with general summaries, will prove especially useful

to the student. His treatment of fossil forms, although brief, will serve as an introduction helpful to those whose schedule does not permit examination of the extensive literature in English or to those for whom the German of Kräusel, Pia, and Hirmer is a serious obstacle. His treatment, in Chapter 10, of recent physiological work will also prove very useful to the student since it comprises significant material usually omitted from algalogical texts, while his survey of symbiosis, even though brief, cannot help but awaken the interest of the reader, and his discussion of the soil algae renders available to the student important material not usually included in texts, yet of considerable biological and practical interest.

As Chapman is primarily an ecologist and his own work, both that done along the coast of Great Britain and that done along our New England coast while he was here as a Henry Fellow, has extended our knowledge of the ecology of salt marshes, the last four chapters, on ecology, notably enhance the value of the book. His discussions of marine and fresh water ecology and especially of the ecology of salt marshes, while in part compilations, are in part original work and throughout show the effective evaluation and interpretation of one thoroughly familiar with the subject.

Finally, his chapter on ecological factors, geographical distribution, and life form, with its encouraging simplicity and directness of presentation, will prove an especially helpful introduction for those to whom this confused and controversial field with its extravagant and elaborate terminology has seemed unduly awesome and discouraging.



FUNDAMENTALS OF PLANT SCIENCE.

By M. Ellen O'Hanlon. *F. S. Crofts and Company, New York.* \$4.25. 9 x 6; xi + 488; 1941.

Having in mind that 70 per cent of the students registered in general botany courses do not expect to continue studies in botany, and that only a small proportion of the remaining 30 per cent will take more than one additional course, the author has prepared her book "to provide for adaptations and certain alternatives, so as to serve several types of courses." The volume is designed for a full year's work, either half of which may be considered a complete course.

The volume is well planned. After the introductory chapters, Part I deals with Classification; The plant as a whole; The plant cell; Leaves; The flower; Fruits; Seeds and seedlings; Roots; and Stems: Part II with Alternation of generations; Algae; Fungi and their allies; Bryophyta; Pteridophyta; Gymnospermae; Angiospermae; Genetics; Organic evolution; and Botanical history. The large number of figures (268) have been carefully chosen and include pictures of famous botanists, beginning with Theophrastus, "the father of the science of botany," and ending with those

of recent times. Brief sketches are included of those who have done pioneer work in the various fields of botany. Suggestions for investigation and discussion and lists of references conclude each section, a lengthy glossary is provided, also a good working index.

For a general culture course in botany and, indeed, for courses designed to provide a foundation for advanced work this volume will be found useful. It is direct in its treatment and stimulating, but it does not confuse the student with controversial problems which the advanced worker is more capable of comprehending.



PLANT HUNTERS IN THE ANDES.

By T. Harper Goodspeed. *Farrar and Rinehart, Inc., New York and Toronto.* 9½ x 6; xvi + 429; \$5.00.

The culmination of the author's search for a lost species of tobacco plant came in an expedition to South America in 1935-36 which was followed by another in 1938-39. The experiences and accomplishments of the members of these two expeditions sent out by the University of California Botanical Garden are described in this book. With his wife and eight North American botanists and assistants the author covered thousands of miles up and down the west coast of the southern continent. In their quest for new and rare ornamental plants, the members of the expedition, motivated largely by the love of plant collecting, were carried from the arid coastal deserts of northern Peru and Chile, through the tropical and temperate rain forests, up the steep slopes of the snowy Andes to the top of the world, Aconcagua (the highest mountain in the Western Hemisphere), and from near the equator on the Ecuadorian border, to far southern Chile—the land of the weird monkey puzzle tree—and out into the South Pacific to Juan Fernandez, "Robinson Crusoe's Isle."

The book contains many excellent photographs illustrating the landscapes and peoples as well as the remarkable vegetation of the Andes. The personal and refreshingly informal fashion in which the story is told makes it interesting and enjoyable reading for the botanist as well as the general reader.



PLANTS COLLECTED BY R. C. CHING IN SOUTHERN MONGOLIA AND KANSU PROVINCE, CHINA. *Smithsonian Institution, U. S. National Herbarium, Volume 28, Part 4.*

By Egbert H. Walker. *U. S. Government Printing Office, Washington, D. C.* 30 cents. 9½ x 6; 563-675 + 7 plates + 1 folding map; 1941 (paper).

In 1932 the National Geographic Society sent Doctor F. R. Wulsin to China to conduct its Central China Expedition. The objective was to collect ethnological, zoological, and botanical material, and to make a

general survey of the region preparatory to more intensive exploration at a later date. R. C. Ching, of the National Central University, Nanking, was chosen as the botanist of the expedition.

Ching gives an interesting account of his travels and experiences, and of the vegetation of the territory surveyed. Over 1,150 botanical specimens were collected, representing 2 families, 12 genera, and 22 species of pteridophytes, and 81 families, 318 genera, and 767 species of seed plants. About 25 new species and varieties have been based on Ching's Kansu specimens. Most of the new forms have already been described in various publications but the present systematic enumeration includes three original descriptions. This list adds much to the previous rather meager knowledge of the flora of this part of China. The work concludes with an index.



HUNGER SIGNS IN CROPS. *A Symposium.*

Edited by Grove Hambridge. The American Society of Agronomy and The National Fertilizer Association, Washington, D. C. \$2.50. 10 x 7; xiii + 327; 1941.

Many so-called plant diseases such as "fired corn," "rust" in cotton, and "die back" in citrus fruit trees are merely hunger signs or symptoms of plant food deficiencies. The purpose of this book is to enable the farmer and other agriculture workers and all interested laymen to recognize the signs of nutritional deficiencies in crops so that they may be in a position to correct the difficulties themselves or seek further expert help from scientific workers in this field. Deficiencies in a considerable number of important crops, such as tobacco, corn and small grains, potato, cotton, vegetables, deciduous fruits, citrus fruits, legumes, are discussed in a practical, understandable manner. Some of the chapters include a key for quickly identifying a deficiency by its symptoms. The excellent plates also simplify identification. Each chapter has a list of selected references and the volume is well indexed.



WORK BOOK IN GENERAL BOTANY. *A Problem Approach to Plant Science Through Observation and Discussion.*

By H. C. Sampson. Harper and Brothers, New York and London. \$1.75. 11 x 8½; vi + 242; 1941 (paper; loose-leaf).

A fourth reprinting of an excellent guide, which first appeared in 1935. It is designed for a two-semester course for college freshmen and is printed on one side of durable loose-leaf sheets, with plenty of space between the topics for the student's notes of observation. Instruction is almost entirely by the question method. Although the general education of the student

has been mainly considered, the completed work will give to those who wish to take advanced courses a sound grounding in basic principles.

The numerous illustrations throughout the text are carefully chosen and well executed. Graphs and tabular matter and reference lists are also provided. There is no index, but the table of contents has been arranged to make textual matter easy to find.



LABORATORY PLANT PHYSIOLOGY. *Second Edition.*

By Bernard S. Meyer and Donald B. Anderson. D. Van Nostrand Company, New York. \$2.00. 10½ x 8½; iv + 101; 1941.

This laboratory manual has been designed on the same basis as the text book of *Plant Physiology* by the same authors. The first part deals with simple experiments in physical and colloid chemistry. The remainder covers very adequately the entire field of plant physiology. Special emphasis is placed on water relations and translocation. A total of 177 experiments are included. The majority of these are of an elementary kind but others introduce more elaborate quantitative methods. The instructor thus may select experiments best suited for elementary and advanced students and for a one or two term course. The book also includes several illustrations of apparatus, descriptions for the preparation of reagents and blank pages for the student's data and notes.

It is the opinion of the reviewer that this is one of the most practical and carefully prepared manuals in plant physiology available in published form.



HOSTS OF THE SUGAR CANE GUMMING DISEASE ORGANISM. *La Revue Agricole de l'île Maurice, Vol. 20, Number 1, 1941.*

By G. Orian. The General Printing and Stationery Company, Port Louis, Mauritius. 9½ x 7; 19-58 + 6 plates; 1941 (paper).

Until fairly recently the gumming disease caused by *Bacterium vasculorum* was known only as a disease of cane sugar. In 1932 the author of the present work studied a disease of maize noticed in Mauritius. The pathogen was found to be *B. vasculorum*. Since that time other investigators have found the white palm to be a natural host for this bacterium on the island. The characters and reactions of the bacteria isolated from these hosts—cane sugar, maize, and white palm—are described. Orian likewise succeeded in inoculating Job's tears, guinea grass, the tall bamboo and the coconut palm with *B. vasculorum*. The results of his experiments with these artificial hosts are presented and illustrated.

VEGETABLE GROWING. Third Edition, Thoroughly Revised.

By James Edward Knott. Lea and Febiger, Philadelphia. \$3.25 net. 7½ x 5½; 356; 1941.

Primarily a textbook for students in agriculture this book will be found of great value to all Victory gardeners, especially those who lack a knowledge of the basic principles and the "why and wherefore" of the various cultural operations. Only when the gardener is well grounded in these fundamental operations is he able to apply the specific cultural methods of each individual vegetable successfully.

This book is a masterpiece in concise, clear diction. The third edition is timely and should be instrumental in increasing vegetable production both commercially and in home gardens.



MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. Volume XXIX, Nos. 179 to 186. Carnegie Institution of Washington Publication No. 525.

Carnegie Institution of Washington, D. C. \$4.50 (paper); \$5.50 (cloth); 11½ x 9; 193 + 56 plates; 1941. The current issue of this valuable series contains 8 papers of considerable interest. The first two are concerned with descriptions and measurements of ova recovered from the rhesus monkey. Hartman and Corner figure two ovarian eggs (two plates) showing respectively the first maturation spindle, and the first polar body and second maturation spindle. Such fortunate recovery has made it possible to demonstrate clearly for the first time that in the monkey, as in the majority of mammals, the first maturation division occurs within the Graafian follicle just prior to its rupture. The recovery of 8 tubal ova of known ovulation age by Lewis and Hartman brings the total number described by them up to 12. Of the new series two were in the 2-cell stage, and six were non-fertile. Attempts to fertilize two *in vitro* proved unsuccessful. One plate of photographs from a motion picture of one of the 2-cell eggs shows the behavior of the centrosphere material before and during early cleavage.

The third paper by Heuser and Streeter is a remarkably complete record of the development of the Macaque embryo beginning with the free blastocyst and ending with the earlier fetal stages. The embryos represent closely over-lapping stages of known ages, accurately oriented and histologically ideal. Such data obtained and handled with superior laboratory facilities are particularly valuable in the interpretation of human material. Realizing that "the embryo at all stages is a living organism and is to be analyzed as a biologic problem rather than purely a morphologic abstraction" the authors have given us more than the customary descriptive study. From this point of

view what were thought to be vestiges of great phylogenetic importance appear to be, in many instances, temporary embryonic structures essential to a particular period of development. The paper is completely and superbly illustrated with 33 plates and 5 text figures.

Three papers deal with human material. Two human ova of the pre-villous stage, having an ovulation age of about 11 and 12 days respectively are described and figured (8 plates, 4 text figures) by Arthur T. Hertig and John Rock. The welcome acquisition of two such beautifully normal ova enable one to complete the hitherto unfinished picture of development in man on the 11th and 12th days following fertilization. Two well-preserved, normal human embryos, one in the primitive-streak stage (Jones-Brewer Ovum I), the other an early presomite embryo having no primitive streak (the Torpin ovum) are described and figured respectively by Jones and Brewer and Joseph Krafka, Jr. The estimated age of the Jones-Brewer embryo is 18½ days. In addition to the primitive groove, allantois, and blood-vessel formation, it has a minute head-process—the earliest stage of the head-process yet described in human material. The Torpin ovum represents one of the best specimens on record of the simple villous group. In placing it in its correct position among the stage II embryos of Group I (Streeter's seriation) interesting comparisons are made with various previously described human ova.

A paper on the "Growth and development of the Orang-utan," by Adolph H. Schultz, with one plate and 14 text figures, supplies much new information on the conditions of growth and development of this important member of the anthropoid apes. Based upon observations and measurements on the outer body and on the skeleton and teeth of large numbers of specimens from many localities, this paper gives us a record of changes which occur with age in the body of the orang-utan. Comparisons, as far as accumulated data allow, show that in general the autogenetic processes of the orang-utan and the chimpanzee are far more similar than are those of either of these apes and man.

In a paper by I. Gersh and Arthur Grelman (3 plates, 1 text figure) a detailed study was made of the vascular pattern in the adrenal glands of rats and mice of various ages and under the influence of various degrees of stimulation (e.g., thyroid feeding, exposure to low temperature). The changes in pattern are interpreted in terms of function, and a physiological basis is established for the specific vascular pattern observed. Deductions are drawn which offer an explanation of the arrangement of the cells into zones in different animal species and under different physiological conditions.

THE RETINA. *The Anatomy and the Histology of the Retina in Man, Ape, and Monkey, Including the Consideration of Visual Functions, the History of Physiological Optics, and the Histological Laboratory Technique.*

By S. L. Polyak. *The University of Chicago Press, Chicago.* \$10.00. 10½ x 7½; x + 607 + 100 figures; 1941.

This book represents a courageous and persistent, not to say stubborn effort, to find an explanation for the complexities of visual function in the complexities of retinal anatomical structure. How successful this effort has been it is impossible for the reviewer to say for the writing is most obscure. Beyond any doubt, however, the author has added many details to our knowledge of the arborization and synapses of the retinal neurones.

What makes the writing so obscure is the effortful and highly unsuccessful attempt of the author to be rigorously critical in his analysis. The "ands, ifs and buts" are piled many stories high, but little distinction made between those reservations that are solidly based and those that are merely frivolous hair splitting. Furthermore, the author fails to apply any critique to the interpretation of the histological pictures that he describes. In the histological technique used, the tissue is killed, some components are precipitated out of its colloidal jelly, others extracted. Upon surfaces which persist or develop through these treatments metal ion films are deposited. The deposition is determined by surface electrical forces which, to say the least, are not identical with those present in the living tissue. These metallic deposits, made visible by reducing the metal ions to the free metal, are examined in histological sections. What the author sees he calls cells, axones, dendrites, synapses, etc. What he actually sees is not tissue components at all but a system of artefacts related in varying ways to structural components of the tissue. This is not to be taken as implying that histological study is meaningless. On the contrary, the point is that histological data have an indirect and variable relation to tissue structure and critical analysis should give different weight to different aspects of the histological picture. Moreover, the author assumes that because certain cell processes appear axon-like while others appear dendrite-like, he can conclude that in the living state nerve impulses travelled away from the cell body in the former, toward the cell body in the latter. Uncritical assumptions of this type lie at the basis of much work in the field of cellular neurohistology and the author might well be pardoned for omitting a discussion of limitations in this field if he were in fact merely presenting a histological study. Such omissions cannot be condoned, however, in a serious attempt to relate structure to function.

In addition to its histological portion, the book contains 130 pages of bibliographical titles which should be extremely valuable to students in this field. There

is also an extensive section on the history of physiological optics which contains many items not readily accessible elsewhere.



A MANUAL OF EMBRYOLOGY. *The Development of the Human Body. Second Edition.*

By J. Ernest Frazer. *Williams and Wilkins Company, Baltimore.* \$9.00. 9½ x 6½; x + 523; 1941.

The stated aim of the author is to provide a connected mental picture of the development of the human embryo. The book's outstanding feature is the application of the regional method so widely used in gross anatomy to a description of embryonic development. The relation of the developing parts to one another and to the whole organism is clearly explained throughout the various transformations. The description is fairly generalized so that the main outlines are not obscured by masses of detailed information. The text is illustrated with numerous well-chosen sections, reconstructions, and diagrams. Changes include such matters as rearrangement and addition of figures, with corresponding revision of the text, and the occasional introduction of new material, as in the case of the foetal circulation.

The book is divided into two parts. The first section deals with the early generalized stages of development, covering such topics as maturation, fertilization, segmentation, implantation, and formation of the embryo, with the establishment of the principal organs and systems. The embryonic membranes and placental circulation are described, and the general aspects of growth and differentiation are considered. The second portion deals with organogenesis, and the history of specific regions and systems. An index is appended, but no bibliography, references being included in the text itself.

This book should be a valuable source of reference for anatomists, advanced medical students and teachers of embryology. The treatment does not seem appropriate for use as an introductory text.



HEARING AND EQUILIBRIUM.

By H. Macnaughton-Jones. *The Williams and Wilkins Company, Baltimore.* \$2.50; 8½ x 5½; vii + 128; 1940.

After two centuries of fairly intensive research by anatomists, physiologists, physicists, and otologists in general, the mechanism of hearing has yet to be satisfactorily clarified. As all know, the main difficulty arises from the smallness of the hearing organ and the remarkable complexity of its structure. To avoid this difficulty the author has proceeded to an investigation by constructing simplified models of parts of the auditory apparatus and on the basis of the models he

seeks to explain some of the characteristics of the phenomenon of hearing. The models are certainly ingenious and a thorough familiarity with acoustics is shown by the author. Unfortunately, the results reported here cover only small and uncoordinated details of the hearing mechanism and the problem of equilibrium is hardly touched at all. With respect to hearing the author features particularly the transmission of the sound wave to the internal ear. In his opinion he demonstrates that the sound wave passes through the pars flaccida of the tympanic membrane to the middle ear and then into the cochlea by means of the round window. This hypothesis, advanced by others years ago, cannot be fully accepted until an explanation of pertinent pathological and experimental observations on man and other animals can be found, for example, the hearing improvement produced by immobilizing the round window, or the hearing loss due only to interference with the ossicular chain. It may be that the author has developed the correct methodological approach to the problem but before his results acquire significance they must be integrated with the knowledge already at hand about the phenomenon studied.



LABORATORY MANUAL IN ANATOMY AND PHYSIOLOGY.
By Caroline E. Stackpole and Lutie C. Leavell. The Macmillan Company, New York. \$1.50. 11 x 8½; 214; 1941 (paper).

This well-organized manual was prepared primarily for use in conjunction with Kimber, Gray and Stackpole's *Textbook of Anatomy and Physiology*, but the exercises are of such a general nature that they can be profitably used with any standard text. The materials are organized around five very broad and logical topics: (1) physiological and anatomical organization and integration; (2) correlation and coordination of external activities; (3) correlation and coordination of internal activities; (4) adaptive responses and the special senses; and (5) reproduction and embryology. Space for student drawings, notes, and comments is included.

Where human material is impractical for dissection and observation, wise use is made of several other vertebrates, notably the frog and the rat. Although some attempt has been made to present the subject from a comparative point of view, this aim has largely been sacrificed to detailed instruction for dissection. The authors' evasion of references to human material in the section on reproduction and embryology is sufficient reason for suggesting that the title "Exercises concerned with human reproduction and embryology" should read "Exercises concerned with vertebrate reproduction and embryology."

The work is outlined in a detailed table of contents, and carries an appendix listing methods for preparing various laboratory materials and apparatus.

PHYSIOLOGY AND PATHOLOGY

IMMUNIZATION TO TYPHOID FEVER. *Results Obtained in the Prevention of Typhoid Fever in the United States Army, United States Navy, and Civilian Conservation Corps, by the Use of Vaccines: Influence of Antigenic Structure and Other Biological Characters of E. typhosa on the Production of Protective Antibodies in the Blood of Immunized Individuals: Increases in Protective Antibodies in the Blood Following the Use of a Single Small Dose of Vaccine for Reimmunization Purposes as Compared with the Use of Three Doses. The American Journal of Hygiene Monographic Series, Number 17, September, 1941.*

From the Research Laboratories of the Army Medical School, Washington, D. C. The Johns Hopkins Press, Baltimore. \$2.50. 9 x 5½; xi + 276; 1941. It is the purpose of this excellent monograph to report in detail a somewhat extensive series of experimental investigations participated in by members of the technical staff of the Medical Department Professional Service Schools, U. S. Army, during the period of 1934-1940, with respect to certain antigenic and immunizing properties of selected strains of *E. typhosa*. These investigations were undertaken with the primary objective of determining whether it might be practicable to still further enhance the protective properties of the typhoid vaccine distributed to the Army and also to discover whether or not the generally accepted hypotheses concerning some of the elements of the immune process might be applicable to the problem of immunity to typhoid fever. The textual material is presented in sections, as follows: Introduction, Historical review of the use of typhoid vaccine in the Army, Navy, and Civilian Conservation Corps, Experimental investigations undertaken, Antigenic characteristics of strains of *E. typhosa*, Relative protective potency of vaccines prepared with virulent and with avirulent strains of *E. typhosa*, Duration of immunity subsequent to immunization with typhoid vaccine, revaccination, and miscellaneous experimental observations. The appendix contains a wealth of descriptive and tabular information concerning techniques, standards, controls, protocols, and bacterial strains used in the experimental procedures upon which the report is based. The book contains a bibliography, but no index. The publication of this report has been awaited with interest and the results of the study made by the Army should have an important bearing on present and future attitudes toward the general problem of immunity and the specific problem of immunity to typhoid fever.



APPROVED LABORATORY TECHNIC; *Clinical Pathological, Bacteriological, Mycological, Parasitological, Serological, Biochemical and Histological. Third Edition.*

By John A. Kolmer and Fred Boerner and Collaborators. D. Appleton-Century Company, New York and London. \$8.00. 9½ x 6½; xxvii + 921; 1941.

Little that is written here could add to or detract from the merits of this widely-accepted and well-established volume of approved laboratory procedures which has already enjoyed three editions within a ten-year period. Here, within the covers of a single book, are found complete, authentic and detailed clinical, pathological, bacteriological, mycological, parasitological, serological, and biochemical methods and techniques. The authors have succeeded throughout in striking a proper balance in the amount of detail given to fulfill the needs of the laboratory technician without being burdensome to the expert. Throughout the book an emphasis has been placed on the importance of using accurate and reliable apparatus and reagents. Special stress is also placed on quantitative tests and reactions, and in qualitative tests an effort is made to suggest a uniform terminology and methods for reporting reactions. Among the many new and approved methods included in this edition (all of which have been placed in the appendix), may be mentioned Quick's methods for the quantitative determination of prothrombin and for the estimation of hippuric acid in the urine, Sparkman's method for the determination of urobilinogen in the urine and feces, the simplified Kolmer complement fixation test for syphilis and the Eagle modification of the Wassermann test, methods for the determination of vitamin C in urine and plasma, and methods for the determination of sulfanilamide and other sulfonamide compounds in the blood and urine. A number of distinguished and experienced authorities are listed as collaborators in the preparation of the book. References are given at the end of some of the chapters, but usually as footnotes. The book is appropriately illustrated with numerous photographs, line drawings, tables, charts, and color plates. A complete index has been provided. This book is enthusiastically recommended to medical students, physicians, teachers, clinical pathologists and laboratory technicians, to all of whom it should prove invaluable.



BEHIND THE MASK OF MEDICINE.

By Miles Atkinson. Charles Scribner's Sons, New York. \$3.00. 9½ x 6½; xiv + 348; 1941.

In the words of the author this book is about "Medicine in its broadest aspects, about its influence on the rise and fall of civilizations as well as about its influence upon the lives and deaths of citizens." The first chapter discusses epidemics as they have affected the course of history. The second chapter is a brief history of the medical arts and sciences of "the Amazing Century: 1840-1940." In Atkinson's opinion the Medical World, like the industrial since the Industrial

Revolution, "is still bewildered by this new-found knowledge which has come so quickly that as yet it has not been properly digested." The author has a sense of humor and the happy faculty of seeing the viewpoint of the doctor and the viewpoint of the patient, and he uses this understanding in the subsequent chapters. These deal with diagnosis and history-taking; prognosis, which includes a sane discussion of euthanasia; clinical medicine, excesses in surgery, the overgrowth of specialism; ethical and unethical practice; the plight of the hospitals, and socialized medicine. Among the specific problems discussed are the amount and kind of explanation the doctor should give the patient with reference to his diagnosis; the "know-it-all" type of patient and the taciturn "you-tell-me" patient; the relative advantages of large and small hospitals; and when the removal of the appendix or tonsils may be harmful. The final chapter on "The Future" closes with the sentences:

This one [civilization] appears to have had its day and to be bent only on its own destruction. . . . At least we can comfort ourselves with the knowledge that, if our present civilization is to die, it has made great strides in the six hundred years of its being, and will hand on to the next a tradition of scholarship worthy of that which Greece and Rome bequeathed to it. And medicine will go on. The sick still have to be tended though the days are dark. Medicine may even prove to be the link that will join the old age to the new.



COMMUNICABLE DISEASE CONTROL. A Volume for the Health Officer and Public Health Nurse.

By Gaylord W. Anderson and Margaret G. Arnstein. The Macmillan Company, New York. \$4.25. 9½ x 6½; x + 434; 1941.

Communicable disease control presents two rather distinct problems—protection of the individual and protection of the community. This volume is written principally from the standpoint of the community. While personal protection has not been neglected, emphasis has been placed on those procedures which are designed to protect the population as a group rather than merely the individual. The authors have kept in mind the problems that confront the health departments, the schools, the visiting nurse associations, and other community agencies. An attempt has been made to evaluate the various control measures as to their relative effectiveness and to outline programs that will yield the greatest return in terms of necessary expenditure. The discussion of control measures is limited to those that are applicable under the conditions which confront the health department, and no effort has been made to consider details or techniques included in hospital care. In the first part of the book, such subjects as the historical considerations, control measures, administrative agencies, the rôle of the public

health nurse, and the legal basis of communicable disease control, are considered. In the second part, the prevention and treatment of the individual important communicable diseases are discussed in detail. A list of suggested readings is placed at the end of each chapter. The graphs and tabular material add to the value of the volume. There is a complete index. This authentic, complete and engagingly-written book should be of considerable value to schools, health departments and other public health agencies for whom it is designed.



DISEASES OF THE BLOOD and Atlas of Hematology: With Clinical and Hematologic Descriptions of the Blood Diseases Including a Section on Technic and Terminology. Second Edition, Revised and Enlarged.

By Roy R. Kracke. J. B. Lippincott Company, Philadelphia and London. \$15.00. 10½ x 7; xxiv + 692; 1941.

During the four years since the first appearance of this now indispensable *Atlas* much new material has accumulated which it has been necessary to incorporate within its pages. The revision and extension includes new material on fractionation of liver extract, a new chapter on hemolytic anemias, a new chapter on hemoglobinuria, new material on the action of drugs on the blood, a new section on hemoglobin and its derivatives as well as the porphyrin compounds, and recent work on bone marrow. The sections on blood transfusion, the operation of a blood bank, and the use of blood plasma have been treated in a comprehensive manner. The revision also includes matter which was omitted from the first volume concerning osteosclerotic anemia, achrestic anemia, ovalocytosis, Hodgkin's disease, and histoplasmosis. A complete section is devoted to vitamin K. In the chapter on the treatment of leukemia recent advances in the use of radiation and radioactive isotopes have been included. The last section (84 pages) is devoted to hematologic technique.

The bibliographies (at the end of each chapter) have been brought completely up to date and new illustrations have been added. There are now 54 colored plates in the volume, and 46 other figures. The index has received the same careful treatment in its revision as has the textual matter.



HISTORY OF PHARMACY. A Guide and a Survey.

By Edward Kremers and George Urdang. J. B. Lippincott Company, Philadelphia, London, and Montreal. \$4.50. 9 x 6; ix + 466; 1940.

The history of pharmacy is really the history of the human race, for in no other phase of human endeavor do we get a clearer picture of man's ingenuity pitted

against the challenge of race extinction than in the development of the art of healing. There has been a real need for a history of pharmacy which would go beyond the mere listing of chronological happenings, and present the subject in a truly integrated fashion. This volume amply fulfils the need. The wealth of material, well organized and completely presented, testifies to the enormous amount of painstaking labor involved in the preparation of the book. The essential facts pertinent to the history of the preparation and use of pharmaceuticals from the days of ancient civilizations, through the dark ages and the renaissance, down to the present day are set forth in concise scientific language and in an authoritative manner. The mutual relationships of pharmacy to medicine, education, industry, and the evolution of society in general are treated in detail. Special note is made of the development of pharmacy in several countries, particularly Italy, Germany, and the United States, while the growth of pharmaceutical schools and societies in this country, and the present tendencies toward uniformity in requirements, professional education, and state board examinations are given special attention.

With an eye toward the possible pedagogic use of the text, the authors have included a bibliography for each chapter, a chronology of pharmacy, a lengthy glossary, and a complete index.



VITAMIN K.

By Hugh R. Butt and Albert M. Snell. W. B. Saunders and Company, Philadelphia and London. \$3.50. 8½ x 5½; x + 172; 1941.

This little volume should be heartily welcomed by physicians and investigators alike, because it presents the pertinent data in relation to one of the most newly-discovered and most important of the vitamins. The authors here set forth in a most acceptable fashion the history of vitamin K, the essential facts with respect to its chemistry and physiologic activity, and such data concerning its clinical use as experience to date has proved expedient. The first part of the discussion is concerned with general information, i.e. the discovery, distribution, methods of preparation and of assay, chemical aspects, and properties of the anti-hemorrhagic vitamin. Then follow, in order, sections on the coagulability of the blood, products which exhibit vitamin K activity, the hemorrhagic diathesis of patients having jaundice, biliary fistula, or hepatic damage, of those patients with certain intestinal disorders, of the newborn infant, and finally, the hemorrhagic diatheses not related to deficiency of prothrombin. The book is illustrated with numerous graphs and tables. A list of 350 important references is given at the end of the volume, and there are complete bibliographic and subject indices available. While intended primarily for the physician and the seasoned investigator, this mono-

graph is a notable contribution to our generally accessible literature on the all-important vitamins, and consequently should be well received in the scientific field.



THE MEDICAL ASPECT OF BOXING.

By Ernst Jökl. J. L. Van Schaik, Ltd. Pretoria.
17s. 6d. 8½ x 5½; 251; 1941 (paper).

It is the author's contention that boxing is a dangerous and, therefore, an undesirable form of physical education. To prove his point he here presents a collection of published case reports, observations and anecdotes dealing with boxing injuries, slight, permanent, or fatal. The physiologic and pathologic changes associated with the various traumae are enumerated and briefly discussed. It appears that lesions of the brain and nervous system are the most frequent, and particularly to be feared since the effects are not immediately manifest. The author realizes that any attempt to abolish boxing, even if the attempt were limited to schools and colleges, would meet with widespread opposition. Hence, he suggests at least more adequate rules regarding ring covering and ropes and the medical supervision of the boxers. Such precautions would still not eliminate the dangers of boxing since "the typical accidents are inherent to the sport as such. . . ." Although one is impressed by the list of cases described they do not constitute definitive evidence to support the author's main plea. However, on the basis of the evidence given the whole subject certainly deserves a serious and thorough investigation.



THE VITAMIN CONTENT OF MEAT.

By Harry A. Waisman and C. A. Elvehjem. Burgess Publishing Company, Minneapolis. \$3.00. 10½ x 8½; ii + 210; 1941 (paper).

The aim of this timely, well-written and thoroughly documented book is to summarize the available information on the nutritive value of meat and meat products. The authors have reviewed the literature in a critical manner and only those results which appear to be most reliable have been included here. Individual chapters are devoted to the more important nutrients and each of the known vitamins comes in for authoritative analysis and discussion. Sufficient fundamental information is supplied in each case so that the value of meat in meeting the requirements of these nutrients can be considered in light of the most recent developments. The daily requirements listed for the individual vitamins and minerals are based on the values recently released by the Committee on Food and Nutrition of the National Research Council. Chapters on the preparation of the samples used and on the proximate analysis of the animal tissues have been

included. A summary chapter is given which presents the general values for the vitamin content of the most important forms of meat products. Appended to each chapter is an extensive list of the literature cited. There is no index. This volume is recommended for its wealth of authentic and useful information on a subject of considerable general interest.



THE ADVANCING FRONT OF MEDICINE.

By George W. Gray. Whittlesey House, McGraw-Hill Book Company, New York and London. \$3.00.
9 x 6; viii + 425; 1941.

This book is appropriately named. It is not concerned with the development of medical theory, but consists almost exclusively of a discussion of such phases of modern medicine as immunities, vitamins, allergies, blood pressure, haemophilia, influenza, sulfanilamide, pain, narcotics, cancer, and senescence. The reader who takes up the volume is not likely to put it down until he has finished it, and then it is probable that he will feel that all those questions that have been accumulating in the back of his mind have been adequately answered.

The thoroughness with which the author has covered his field is evidenced by the number of medical authorities whom he consulted and to whom he acknowledges his gratitude; the list of names covers more than four pages. There is also an extensive catalog of recommended reading and seventeen pages of index.

In one instance the author is guilty of a misstatement—this is when he states that George Fox was an epileptic. Fox was inclined to hysteria, and on one occasion suffered from an attack of hysterical blindness that lasted several days, but his biographers are agreed that he was not a victim of epilepsy in any sense. But this is a mere detail which does not detract from the value or interest of the book.



ENDOCRINOLOGICAL STUDIES IN THE BLUE WHALE (BALAENOPTERA MUSCULUS L.). *Hvalrødets Skrifter, Scientific Results of Marine Biological Research, No. 24.*

By Alf P. Jacobsen. Jacob Dybwad, Oslo. Kr. 8.00. 10½ x 7; 84 + 8 plates; 1941 (paper).

The endocrinology of the cetaceans is an entirely virgin field of investigation, hence the present studies on the blue whale are a noteworthy contribution. The data herein presented were collected over a period of six years, during which time the author travelled as surgeon with a floating factory in the whaling areas of the antarctic. The investigation includes discussions on the gross and microscopic anatomy of the pituitary, thyroid, pancreas, adrenals, ovaries, and testes of the blue whale. A sufficient number of measurements and weights of the various organs is given to arrive at a

fairly definite idea as to their size. The investigation is concerned further with the preparation of various pure hormone extracts from the whale endocrines, and a study of their biological potency as compared with those from other animals. The fact that the whale endocrines were found to be quantitatively and qualitatively equal to the corresponding glands from cattle is ample reason for believing, as the author does, that the blue whale represents an enormous potential source of numerous important pharmaceuticals.

The monograph lists a bibliography of 101 titles, and carries a detailed table of contents. Numerous graphs, charts, tables, and photographic plates are presented in support of the textual material.



THE MICROBE'S CHALLENGE.

By Frederick Eberson. *The Jaques Cattell Press, Lancaster, Pa.* \$3.50. 10 x 7; viii + 354; 1941.

Bacteriology as a science is not a subject dealing with static or fixed organisms following a uniform pattern of existence. Because of the recognition of this fact many important modern discoveries have been made. In like recognition of this fact, the dominant theme of this book is microbe *versus* man. In the same sense, it is the challenge of the microbe. The purpose intended is to narrate some of the highlights in the history of preventive medicine and to bring together in a logical form the fundamental principles upon which the modern bacteriological control of infectious diseases is based. Wherever possible, attempts have been made to clarify further the meaning of some technical terms by the use of word pictures or analogies. The author tells his story simply, honestly, and effectively. He believes that we have only just begun our battle with microbes, and his thesis seems to be that microbes are highly adaptable living things and that their adaptations, like those of other living things, tend toward their survival. Many of us do not realize how effectively microbes resist destruction. Particularly interesting are the author's discussions of the changeable characters of microbes, the startling discoveries regarding their chemistry, and the analysis of what constitutes their life and death. There is a short glossary, a list of suggested readings, and an index. Scientific specialists and intelligent layman alike will find the book fascinating and challenging—a thoroughly satisfying piece of reporting.



MICROBES WHICH HELP OR DESTROY US.

By Paul W. Allen, D. Frank Holman, and Louise Allen McBee. *C. V. Mosby Company, St. Louis, Mo.* \$3.50. 8½ x 5½; 540 + 13 plates; 1941.

The stern necessities of life sooner or later lead us all by the route of cruel experience to understand that

microbes have major rôles to play in the production of health, homes, food, clothes, fuel, and defense. In living, we must make use of, and defend ourselves against, many powerful agencies, and a solid knowledge of microbes is necessary if we are to avoid disease, hunger, exposure and oppression. This book, then, may be considered as the product of the average layman's need of becoming "microbe conscious." The authors have compiled here an amazing amount of information about man and his microbe friends and enemies. Some of the more interesting chapters have to do with the age of superstition, making the world microbe conscious, surgeons and microbes, the struggle against diphtheria, virus diseases, appendicitis, food poisoning, food preservation, friendly microbes, infections and sanitation on fur farms, and the bacteriophage. In addition, each of the common diseases caused by bacteria or viruses is discussed in detail. The illustrations, especially the series of 13 colored plates, are particularly well chosen. A carefully selected bibliography is appended to the book and an index has been provided. All in all, this interesting presentation of bacteriologic information should have a wide appeal to the general reader.



HANDBOOK OF COMMUNICABLE DISEASES.

By Franklin H. Top and Collaborators. *The C. V. Mosby Company, St. Louis.* \$7.50. 9 x 6; 682; 1941.

This complete, authoritative and well-written book is intended as a text or handy reference for all persons whose professional duties necessitate contact with certain communicable diseases or infestations. An attempt has been made to present the material in as concise and handy a manner as possible. The chapters on pneumococcic pneumonia, tuberculosis, syphilis, and gonorrhea are somewhat longer than would be anticipated in a handbook, but the paramount importance of these diseases from both a curative and a preventive standpoint would seem to justify the additional space accorded them. The various diseases discussed have been classified by common portal of entry, a method which is unusual but one that should prove helpful. Under the respiratory portal of entry, the diseases have been further classified alphabetically into those caused by bacteria and those caused by viruses. Two chapters of unusual interest are concerned with the management of communicable diseases in the home and in the hospital. The book is illustrated with excellent clinical photographs and a series of ten color plates. A list of helpful references for further reading is appended to each chapter in the book. The appendix provides in tabular form much valuable data on associated conditions and complications and differential diagnosis. A glossary and a complete index conclude the volume.

ANNUAL REPORT FOR THE YEAR 1940: DIVISION OF TUBERCULOSIS CONTROL. *The Bulletin of the British Columbia Board of Health. Volume 11, Appendix No. 1, 1941.*

By W. H. Hatfield. Provincial Board of Health, Victoria, B. C. 10 $\frac{1}{2}$ x 8 $\frac{1}{2}$; 166; 1941 (paper).

This document includes descriptive, statistical and pictorial presentations of the work being done in the fight against tuberculosis in this particular province of Canada. The introduction discusses such matters as case finding, treatment, follow-up work, rehabilitation, finances, health education, and the work with the Indians in the province. Then follow sections dealing with the district nursing program, social service, travelling clinics, and the Vancouver, Tranquille and Victorian units. The statistical portion of the report presents an extensive series of tables and charts concerning the institutional admissions and discharges, clinics, new cases examined, notifications of tuberculosis, and the comparative analysis of case status. There is a list of maps showing the incidence, distribution and mortality rates of tuberculosis in the province, and the report concludes with a special series of charts graphically illustrating the number of pneumothorax treatments, new and old cases examined by all clinics, x-ray examinations, the percentage distribution by age groups, the racial distribution, the total deaths from tuberculosis, and much other pertinent information. The volume is not indexed.



THE VALUE OF HEALTH TO A CITY. *Two Lectures Delivered in 1873 by Max Von Pettenkofer. Reprinted from Bulletin of the History of Medicine, Vol. X. Nos. 3 and 4, 1941.*

Translated from the German, with an Introduction by Henry E. Sigerist. The Johns Hopkins Press, Baltimore. \$1.00. 10 $\frac{1}{2}$ x 6 $\frac{1}{2}$; 52; 1941.

As many public health administrators have from time to time realized there is apparently only one way besides an epidemic to move communities and countries to expend funds on preventive health measures. It is to point out, step by step, how such measures will eventually bring about financial returns in terms of more man-hours of work, and less sickness compensation, welfare aid, etc. In these two lectures delivered about 70 years ago at Munich Pettenkofer followed just this line of reasoning in pleading particularly for an adequate water supply system. He further bolstered his argument with an appeal to civic pride by emphasizing the lower mortality of London (which by that time had its water supply) in comparison with that of Munich. The author's cogent reasoning is valid to-day as it was then but otherwise these lectures cannot be considered as outstanding examples of Pettenkofer's contributions to medical science. As a matter of fact, Sigerist's introduction

which includes a sketch of Pettenkofer is much more interesting reading.



ESSENTIALS OF ENDOCRINOLOGY.

By Arthur Grollman. J. B. Lippincott Company, Philadelphia and London. \$6.00. 9 x 6; xiv + 480; 1941.

In this book a critical evaluation of all important aspects of the subject of endocrinology is attempted. Following a brief, initial chapter in which a basic survey of the field is made, the material is presented in five parts. In Part I, Endocrine glands of the cranial cavity, the bulk of the discussion is devoted to the hypophysis in its anatomical, physiological, pharmacological and pathological aspects. There is a brief discussion of the pineal gland. Part II, The branchiogenic organs, is devoted to the thyroid, the parathyroids and the thymus. In Part III, The endocrine organs of the abdominal cavity, the islet tissues of the pancreas and the adrenal glands are discussed. Part IV, The hormones of the reproductive Systems, includes a lucid and thorough presentation of this complicated field. In Part V, The hormones derived from the nonendocrine organs, a brief survey is made of current knowledge of hormones of the gastro-intestinal tract and other presumptive hormones (cardiac, liver extract, renal extract, heparin, etc.). Lists of pertinent references are appended to each chapter and there is an index. The book is illustrated with 74 figures.



A HISTORY OF MEDICAL PSYCHOLOGY.

By Gregory Zilboorg in Collaboration with George W. Henry. W. W. Norton and Company, New York. \$5.00. 9 $\frac{1}{2}$ x 6; 606; 1941.

This excellent history of medical psychology is the result of a sixteen-year period of collecting and digesting basic and illuminating data. The material is presented throughout in the context of the social and ideological culture characteristic of the various periods described. Crucial advancements are highlighted, so that the book is not merely a catalog of contributors and their contributions, but an intelligibly molded formulation of the dynamic forces which have culminated in the present-day concepts dominating this important field of human thought. There are fourteen chapters in all. The first twelve, written by Zilboorg, present a survey of medical psychology from primitive to modern times. The last two chapters, by Henry, are concerned with a brief account of the history of the differentiation of organic from functional mental disorders and with the transformation of asylums into hospitals. References are given in footnotes and there is a well-planned index.

BIOCHEMISTRY

CHROMATOGRAPHIC ADSORPTION ANALYSIS.

By Harold H. Strain. Interscience Publishers, Inc., New York. \$3.75 9 x 6; x + 222; 1942

Many important advances in the natural sciences have depended upon the detection and isolation of specific, homogeneous chemical compounds. Chromatographic adsorption analysis is the separation of compounds with the use of selective adsorption. This powerful tool of analytical and synthetic research has remained much of a mystery to many because of the lack of a simple approach to the subject, which this book now affords. The importance for the biochemist of gentle methods of analysis and separation such as chromatographic adsorption analysis, electrophoresis, and ultracentrifugation which might be used on the labile compounds with which he works cannot be over emphasized.

Here is a simplified explanation of the theory, a very suggestive presentation of the many uses of the method for structural, inorganic and organic chemists, a first hand account of the careful techniques (including simplified illustrations of apparatus, formulae, and tables) and a very large bibliography (40 pages), all of which combine to make this an important handbook for workers in research and industry alike.



SEX

WOMAN'S PERSONAL HYGIENE; MODERN METHODS AND APPLIANCES.

By Leona W. Chalmers. Foreword by Winfield Scott Pugh. Drawings by Alfred Feinberg. Pioneer Publications, Inc., New York. \$2.00. 8 x 5½; xii + 192; 1941.

After a brief description of the anatomy of the female organs associated with reproduction the author proceeds with her discussion of "intimate domestic hygiene." Included are such subjects as menstrual pain, leucorrhea, social diseases, vaginal hygiene, plastic surgery, etc. The specific value of the book lies in the intelligent descriptions of such procedures as enemas, vaginal douches, and postpartum and other exercises. The author is a physician's wife who has devoted many years to the study of feminine hygiene. Her book is simply and clearly written with little use of technical language, except in some quotations from medical authorities which she used to add authoritative weight and to reassure the reader with regard to some of her statements. It is written for the laywoman and the attitude taken is one of common sense.



BIOMETRY

THE HEARING OF SCHOOL CHILDREN. *A Statistical Study of Audiometric and Clinical Records. Mono-*

graphs of the Society for Research in Child Development, Vol. VI, Serial No. 29, No. 3.

By Antonio Ciocco and Carroll E. Palmer. Society for Research in Child Development, National Research Council, Washington, D. C. \$1.00. 9 x 6; v + 77; 1941 (paper).

A report of a detailed summary of the results of an investigation which the U. S. Public Health Service has conducted on the hearing of Washington, D. C. school children over a 5-year period, beginning in 1931. Some of the findings have already been published but are herein included. The aims of the study were:

First, to evaluate critically certain methods employed in studies of deafness in children. Second, to determine the degree of hearing impairment and the clinical and other factors associated with it. Third, to formulate a program which, it is hoped, will permit a conclusive contribution toward the solution of the problem of prevention of deafness.

Very nearly 14,000 children were examined with a Western Electric 4-A (phonograph) audiometer and over 1,400 children received a hearing test with a Western Electric 2-A (pure-tone) audiometer. About one half of the children in the latter group were examined twice, and over a third received three tests. Although the phonograph audiometer is satisfactory under laboratory conditions the results of the tests in the school environment seem to indicate that effort should be directed towards improving the instrument and methods of testing before the most satisfactory results can be obtained if a program aimed at the prevention of deafness in children is to be developed in the schools. During the 5-year period "fully 30 per cent of the ears with only a slight high tone loss and 25 per cent of ears with slight loss of tones of the conversational range deteriorated sufficiently to acquire a marked degree of the respective impairment." The rate of development of decreased perception for the tones of speech is greater in the younger than in the older children. In this type of impairment, in almost one half of the ears there was also present an overt and marked alteration of the otoscopic appearance of the tympanic membrane. The study points to the importance of therapeutic care as well as the prevention of middle ear infection. Tables and graphs exhibiting the results of the tests, form blanks, and a bibliography of 66 titles are included in the report.

STATISTICAL METHODS FOR RESEARCH WORKERS. *Eighth Edition, Revised and Enlarged.*

By R. A. Fisher. Oliver and Boyd, Edinburgh and London. 16s. 8½ x 5½; xv + 344. 1941.

With the eighth edition of this textbook, the form and contents seem to have become more or less stabilized. One notes very little revision or further expansion of the preceding edition (cf. Q. R. B., Vol. 14, p. 264).

The 16 years that have passed since the work first appeared have seen changes in the viewpoint and attitude of statisticians towards the methodologic developments formulated by Fisher as well as to the contents of this work. With time and with the aid of texts published by others the confusion of ideas engendered in part by Fisher's unique expository style has to some degree lessened. Although for the uninitiated this will always be a difficult book, the more advanced student of statistics is enabled to find in it a clearer outline of the objectives of the recent analytic techniques than in the many other texts which presumably are prepared for elementary courses on the subject.



FAMILY EXPENDITURES IN THE UNITED STATES. *Statistical Tables and Appendices.*

By the National Resources Planning Board. United States Government Printing Office, Washington, D. C. 50 cents. 11½ x 9½; xxi + 209; 1941.

This, the third in a series of reports prepared by the National Resources Planning Board on the basis of data from the 1935-36 Study of Consumer Purchases

is the most detailed analysis yet made of family expenditures in the United States and includes a breakdown of these expenditures into over 90 categories of outlay, together with comparative estimates indicating farm, rural nonfarm, and urban differences, regional variations, and differences with respect to size of family, as between white and Negro families, and in relation to expenditures for durable goods. The statistical results are shown in the present volume both in summary form and in a more detailed set of reference tables. A description of the sources and methods used in the study is presented in an appendix.

THE BULLETIN OF MATHEMATICAL BIOPHYSICS. *Volume 4, Number 2, June, 1942.*

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: A mathematical analysis of elongation and constriction in cell division, by H. D. Landahl; A fundamental form for the differential equation of colonial and organism growth, by Nathan W. Shock and Manuel F. Morales; A note on the diffusion of electrolytes in cells, by Alston S. Householder and Robert R. Williamson; Periodic phenomena in the interaction of two neurons, by George Sacher; A theory of electrical polarity in cells, by Robert Williamson and Ingram Bloch; An alternate approach to the mathematical biophysics of perception of combinations of musical tones, by N. Rashevsky.



PSYCHOLOGY AND BEHAVIOR

SELF-DIFFERENTIATION OF THE BASIC PATTERNS OF COORDINATION. *Comparative Psychology Monographs, Volume 17, Number 4, Serial Number 88.*

By Paul Weiss. *The Williams and Wilkins Company, Baltimore.* \$2.00. 10 x 6½; 95; 1941 (paper).

This paper is a contribution to the study of the problem of the ontogeny of motor coordination. Its stated objective is "to present direct experimental proof that the basic patterns of coordination arise by self-differentiation within the nerve centers, prior to, and irrespective of actual experience in their use". The experiments of the author which are analyzed with respect to their bearing on this matter, deal with the transplantation of limbs in amphibians. Weiss has previously shown that the transplantation of limbs in young amphibians, in such a way as to provide the transplant with motor innervation from a nerve branch of one of the normal host limbs, results, after transmissive connections have been established, in contraction of the muscles of the supernumerary limb *concurrently* with the contraction of the corresponding muscles of the normal limb. The phases of activity of a supernumerary muscle correspond precisely with those of the synonymous muscle of the host limb innervated from the same plexus. In the present work this "homologous response" of synonymous muscles or, as the author now proposes to call it, this "myotypic" response, has been utilized as an assay method.

In larval salamanders possessing functional limbs the two fore limbs were exchanged with the original dorso-ventral orientation retained. Since the two limbs are mirror images of each other, this operation amounts to replacing one limb by another which has the same assortment of muscles but in exactly the reverse arrangement. After reinnervation the action of these limbs was studied by means of slow-motion pictures; and "myochronograms" giving the details of the activity of each muscle were constructed. This study revealed that, in the transplanted limbs the muscular movements were such as to indicate that the nerve centers were calling the individual muscles into action in the same rhythm, sequence and intensity as they had done when they were still operating normal legs with unreversed musculature. In doing this, however, the peripheral effects were just the opposite to those which would serve the organism; instead of progression, they produced regression. Nevertheless, this behavior was never altered by any adaptive change even though the animals were kept for long periods of time.

Similar experiments done with amphibian larvae in which the limbs were transplanted before the onset of function led to similar results. Such limbs, from the very onset of motility, moved in reverse. This indicates that the basic coordination patterns revealed in the previous experiments are not only ingrained in the centers after they are developed, but that they are originally developed without any constructive influence of experience. The centers develop and elaborate the patterns of coordination by pure self-differentiation. That sensory control plays no constructive rôle in the development and maintenance of these basic patterns

of motor coordination has been shown by further experiments dealing with de-afferentiation of limbs.

Weiss concludes that the basic repertoire of primary motor patterns exhibited by these forms arises by self-differentiation within the central nervous system independent of sensory control and guidance by experience. These patterns when later projected into an anatomically normal peripheral effector system, produce biologically adequate effects. If, however, they are confronted with an anatomically disarranged periphery they produce correspondingly distorted effects without signs of corrective adjustment.

The experiments upon which these conclusions are based are presented with the utmost clarity and the results seem to be unequivocal. The author has been very careful to distinguish between the factual content of the experiments and any speculative hypotheses derived from them. This clear-cut distinction makes it easy to evaluate the evidence presented, quite apart from its theoretical implications. When this is done, it seems to this reviewer that the author's fundamental conclusions concerning self-differentiation of the basic motor patterns are amply supported by the experimental results; are, in fact, almost inescapable. It must be emphasized, however, that the work applies specifically to the amphibia and that, as Weiss himself points out, the situation in higher vertebrates and particularly in higher mammals forms quite a separate problem. Some work on mammals which does bear upon the problem of motor coordination is briefly reviewed in this paper and Weiss believes that, despite the enormous number of acquired secondary patterns learned under the guidance of cortical activity which tends to obscure the old primary patterns in this group, here, too, such basic unlearned patterns do exist.



THE PSYCHOLOGY OF ARISTOTLE: *An Analysis of the Living Being.*

By Clarence Shute. Columbia University Press, New York. \$2.00. 8½ x 5½; ix + 148; 1941.

Some years ago H. G. Wells stated that in general one could learn more about the world's great books by reading commentaries upon them than by reading the originals. Without committing ourselves to the acceptance *in toto* of such a broad statement, we can yet realize that it seems applicable to Aristotle's writings on psychology. This is partly because these were not integrated by the original author; they are scattered through five different documents.

The compiler of the commentary, like most modern students, perceives clearly the relation between psychology and biology, and believes the appreciation of the former to involve some general knowledge of the latter. Therefore he has carefully sifted all the biological and metaphysical works of Aristotle in order to glean material which he may consider indispensable

to an intelligent comprehension of that writer's theories of the mental processes of man.

The quotations, however, are only the foundations on which the author has erected his own superstructure, which is a commentary on the development of human mentality, its resemblances and dissimilarities to that of the lower animals, the relation between mental and physiological activity, and finally the immortality of the soul. Whether Aristotle himself would have approved of this procedure is irrelevant; The Stagerite was the product of his age, and his thought was conditioned by his environment. Notwithstanding that for twenty centuries he dominated all fields of human thought, he yet needs an interpreter to be understood by modern minds—or rather, modern minds need an interpreter to understand him—and this need is well supplied by the present book. The reader who has assimilated it will be the better qualified to read Aristotle in the original for having done so.

There is an index of eight pages and an appendix containing an Analytical Outline of the same length.



SOCIAL INFLUENCES AFFECTING THE BEHAVIOR OF YOUNG CHILDREN. *Monographs of the Society for Research in Child Development, Vol. VI, Serial No. 28, No. 2.*

By Ruth Pearson Koshuk. Society for Research in Child Development, National Research Council, Washington, D. C. \$1.00. 9 x 6; iii + 71; 1941 (paper).

In the present survey, which the author states is far from exhaustive, an effort has been made "to place in reasonable perspective the significant research publications since 1925 dealing specifically with the influence of social factors, broadly defined, on the behavior of young children. A number of unpublished studies known to the writer are included." The extensive literature concerning handicapped children is not included, nor are systematic psychologies, texts, and works of a popular nature, with a few exceptions. The discussions of the literature are grouped under four main headings: A. Social influences ignored or minimized; B. Social influences recognized but deplored; C. Social influences recognized: Suggestions for research, basic concepts, and method; D. Studies relating social influences to child behavior. Section D is broken down into ten categories, some of which we give, selected at random: Ecological studies and census-type surveys of social backgrounds; Comparison of behavior before and after marked environmental change; Mental growth careers and the predictive value of early tests; Experiments in social interaction:—observation under relatively controlled conditions; Longitudinal or genetic studies.

In a summary the author gives her interpretation of the direction in which studies of child development

and behavior are moving as revealed by her analysis of the literature. The extent of the literature covered is indicated by the list of 525 titles given in the bibliography. There is no index.



PSYCHOGENIC FACTORS IN BRONCHIAL ASTHMA. *Parts I and II. Part I. Psychosomatic Medicine Monograph IV. Part II. Psychosomatic Medicine Monographs, Volume II, Nos. I and II.*

By Thomas M. French and Franz Alexander and Collaborators. National Research Council, Washington, D. C. 10½ x 6½; Part I, 92: \$2.00. Part II, 236; \$3.00 (paper).

This *Psychosomatic Medicine Monograph* embodies the results of a four-year cooperative study by the research staff of the Chicago Institute for Psychoanalysis with the assistance of four physicians specializing in allergy, of both psychogenic and allergic factors, found in patients with asthma. The first chapter is devoted to a discussion of asthma from the point of view of the allergist, and the second and third to a review of the literature on psychogenic factors in asthma. The remainder of the monograph presents the findings in 27 cases of asthma treated by psychoanalysis. The outstanding findings prominent in these cases may be summarized as follows: 1. The central emotional problem concerns separation from the mother. 2. There is a relation of asthma to suppressed crying for the mother. 3. The mothers of asthmatic children belong to the rejecting mother type. 4. Some mothers of asthma children show a marked pride in their children's early independence. 5. Asthma attacks often appear in very early childhood. 6. The sexual impulse seems to be most significant in precipitating asthma attacks. 7. Allergic patients, after they succeed in overcoming their emotional conflict about emancipation from the mother or her substitute, become more resistant against the allergens. Part II is devoted to a detailed presentation of the cases, including the course of the analysis, on which this study is based. The entire study is thoughtfully carried out and the stimulating findings are discussed in a conservative way. There is a bibliography of 43 titles.



INTELLIGENCE, POWER AND PERSONALITY.

By George Crile. Whittlesey House, McGraw-Hill Book Company, New York and London. \$3.00. 9 x 6; vi + 347; 1941.

In this book the author presents the results of a comparative anatomical and physiological study of the energy-controlling system of man and animals, notably the brain, the heart and the blood, the thyroid gland, the adrenal glands, the celiac ganglia, and the sympathetic system. He postulates that variations in intel-

ligence, power, and personality among the different species of animals and the races of man are determined by variations in the relationships of these organs to each other. In all, 3,734 animals, collected in the past ten years from all parts of the world, form the material of the study. The organs of each animal were weighed and weights relative to each other and to the total body weight computed. These data are presented in detail in tabular form in the appendix. The viewpoint throughout is mechanistic. The terms comprised in the title are used broadly and without any attempt at precise differentiation, "intelligence", for instance, being equated with relatively heavier brain weight, "power" with a relatively highly-developed sympathetic system, etc. The validity of the method which is used of comparing absolute organ weights of one animal of a species and one animal of another species, and drawing general conclusions as to the relative intelligence, power, and personality endowment of the two species is questionable. Nevertheless, the amazing mass of unique information presented is absorbing. In Part IV, Summary and conclusions, ten biological principals which the author believes account for the unique and variable intelligence, power, and personality of man and animals are listed and discussed. The book is indexed but does not include a list of references.



SOCIAL LEARNING AND IMITATION.

By Neal E. Miller and John Dollard. Yale University Press, New Haven; Oxford University Press, London. \$3.50. 9 x 6; xiv + 341; 1941.

In this book imitative learning, as an item of human behavior, is studied from the double viewpoint of the psychological principles involved in its learning, and the social conditions under which this learning takes place. The first five chapters are devoted to a consideration of the learning process in general. Four basic factors in all learning are discussed, notably *drive*, *cue*, *response*, and *reward*. Beginning with chapter six, imitative behavior is the focus of attention. Three sub-mechanisms are described: *some* behavior, *matched-dependent* behavior (leader-follower relationship) and *copying*. Two experimental studies of imitative behavior are reported, one carried out on rats and one on children. The results in both cases demonstrate that imitation of a given response will be learned if rewarded, and generalized to new, somewhat similar situations. One chapter is devoted to a detailed discussion of matched-dependent behavior, and one chapter to copying with particular attention to the rôle of difference and sameness. A chapter of particular interest is that on social conditions producing imitation. Crowd behavior is discussed in the light of the tenets of the preceding chapters and on analysis of a lynching presented. There are two appendices,

the first devoted to a critical review of Holt's theory of imitation, and the second summarizes briefly (a) theories of other writers on the nature of imitative behavior, and (b) other experimental work on imitative behavior. There is an eight page list of references and an index.



INTRODUCTION TO PSYCHOBIOLOGY AND PSYCHIATRY.
A Textbook for Nurses.

By *Esther Loring Richards*. C. V. Mosby Company, St. Louis, Mo. \$2.50. 8½ x 5½; 357; 1941.

Out of her long experience in teaching the undergraduates of The Johns Hopkins Training School for Nurses, Doctor Richards has written this welcome and excellent textbook. The intention of the book is to promote an understanding of human behavior in its relationship to the practice of the nursing profession. The material is presented in two parts. Part I, Psychobiology—A study of the functioning in normal behavior, presents the fundamental concepts of the psychobiological viewpoint in the context of its historical position in man's way of looking at himself. The personality study, by means of which the nurse is given an opportunity to take stock of the personality equipment with which she lives, is discussed in detail.

Part II, Psychiatry or psychopathology, is devoted entirely to a descriptive presentation and discussion of the various reaction types which comprise the clinical material of psychiatry. Two chapters are devoted to the minor reaction types, or neuroses, and the remainder of the book to the major reaction types, or psychoses. The classification followed is that developed by Adolph Meyer. The discussion throughout is simple and lucid. A list of references is appended to each chapter and there is an index.



CHILDREN IN A WORLD OF CONFLICT.

By *Roy F. Street*. The Christopher Publishing House, Boston. \$2.50. 7¼ x 5¼; 304; 1941.

This book has been prepared especially for the benefit of teachers and parents but will be found generally useful. The main theme is that in his daily life the child continuously encounters an environment which always possesses some new and strange qualities. Unless he is well equipped to meet these unusual conditions he may react through fear, surprise, or ignorance in a manner that does not meet the approval of the adult moiety. Therefore, the author pleads for a better understanding of the limitations of childhood and a greater flexibility in teaching methods both for school and home. To illustrate his point of view the author presents short case histories to describe the several types of childhood personality and the so-called problem children, and outlines pedagogic methods to

overcome the difficulties. The style of writing as well as the author's obvious mastery of the subject serve to render this book effective for its purpose.



UNDERSTANDING YOURSELF. *The Mental Hygiene of Personality. Sixth Edition, Revised.*

By *Ernest R. Groves*. Emerson Books, Inc., New York, \$2.50. 8 x 5½; 279; 1941.

This book, which is now issued in a sixth and revised edition, presents a practical and common sense discussion of the mental hygiene of personality, designed to be useful to the average reader. The essence of wholesome personality is regarded as learning to live with one's self and to make good use of all one has for adjustment to the environment. The author's main and sound thesis is to know one's self as one is, accept one's self as one is, and on this basis utilize one's self to the utmost. The book is written in a simple, direct, unpretentious style. It should prove of interest to almost any adult reader.



**DE OMNIBUS REBUS
ET QUIBUSDEM ALIIS**

CARNEGIE CORPORATION OF NEW YORK: REPORT OF THE PRESIDENT AND OF THE TREASURER for the Year ended September 30, 1941.

By *Frederick P. Keppel and Robertson D. Ward*. Carnegie Corporation of New York, New York. 9 x 6; 148; 1941 (paper).

The Carnegie Corporation of New York was established by Mr. Carnegie in 1911. It has for its purpose the advancement and diffusion of knowledge and understanding among the people of the United States and the British Dominions and Colonies. In addition to a review of the 1940-41 year's work, Keppel, who retired in November, gives an interesting survey of his nineteen years of service as president. He does not hesitate to point out where mistakes have been made. Comparing the general picture in 1941 with that of 1922, he says:

... the following changes seem to the writer to be the most significant. In the first instance the place of the foundation in the whole picture of what may be termed cultural philanthropy has definitely changed. ... While the total capitalization of foundations has risen, ... the total income available for distribution annually has fallen. As to other sources of support, individual gifts are, for the present at any rate, dropping off, while public funds and the services and gifts of industry are furnishing a rising share of the total contributions. Foundations no longer avoid fields which will bring them into contact with government or business, but are eager to seek the cooperation of both.

In 1922 foundation funds went predominantly to academic or quasi-academic recipients. Today there is a much wider spread. It is today realized that a

grant which helps only a single institution is not an ideal grant, and for that reason exemplary influence, or prestige if one prefers, is today deliberately given more weight in the selection of institutions than financial need.

... During these nineteen years the individual rather than the curriculum or the academic machinery has become the center of our thinking. More and more of our education is taking place outside the classroom. Libraries, museums, and other various agencies are cutting into the territory hitherto controlled by school or college. In all this the progress of adult education has been an important factor.

In 1922 the foundation was confident of its place of usefulness. It still has confidence today, but of a different kind. It has less trust in what money can do, far less certainty of its own wisdom, but it knows from experience that, while many of its most cherished plans may go astray, others will prove useful to humanity to a degree far beyond original hopes.

WORKING WITH THE MICROSCOPE.

By Julian D. Corrington. *Whittlesey House, McGraw-Hill Book Company, New York and London.* 1941. 9 x 6; xi + 418; \$3.50.

Most books written for the purpose of providing instructions in microtechnique fall into one of two classifications—either they are frankly juvenile and unscientific or they are highly professional and technical. The author has prepared this manual for the large body of serious workers who fall in between these two extremes. Beginning with the simplest and proceeding by easy stages to advanced operations, the explanations have been made as detailed and nontechnical as possible. The volume not only tells the beginner how to use the microscope itself, but gives complete instructions on the preparation of slides or specimens of every degree of difficulty. Nearly every type of subject and field of interest is treated—from microfossils to textiles, from pond life to photomicrography, from soils to sections. In addition to the material on the preparation of slides, the book contains useful information about the microscope and its accessories, new methods in microscopy, short cuts, and special problems. The final chapter, giving full directions on the preparation and use of reagents, is especially valuable. The book is illustrated with many carefully-chosen photographs and line drawings. The appendix contains a list of sources of supplies, a bibliography, and reference tables. A complete index concludes the volume.

Working with the Microscope is heartily recommended as of interest to every amateur, hobbyist, and student—to everyone except the advanced professional—who wants to learn something of this fascinating science.



THE UNIVERSAL CONSTANT IN LIVING.

By F. Matthias Alexander. *With an Appreciation by G. E. Coghill.* E. P. Dutton and Company, New York. \$2.50. 7½ x 5; xiii + 270. 1941.

After an honest attempt of three months duration to sift the verbiage of these pages for the point the author is trying to make, the reviewer must finally accept defeat, and admit that the *Universal Constant* is as elusive as the end of a rainbow. An understanding of the work should not be attempted by anyone who is less than a mental giant, because, to lesser minds, the strain of 260 pages of sentences similar to the following will undoubtedly lead to untold mental anguish.

The close connexion which I observed to exist between the processes of use and functioning, and which worked as I saw from the whole to the part, was sound evidence to me of an integrated working of the organism, and when in working to this principle I discovered the existence of a control of this integrated working, which, according as it was employed, influenced for good or ill my general functioning, I realized that I had not only come upon the primary control of the integrated working of the psycho-physical mechanism in the use of the self that I needed to bring about a change in my own reaction, but that, by the objective proof emerging from my observations and the procedures I employed, the concept of the organism-as-a-whole had been placed upon a foundation that could be scientifically established.

The author admits that it is as difficult for him to put his concept into spoken or written language as it is to describe the sensation red. This being the case, until a suitable mode of communication has been discovered, it seems useless for anyone to make such an attempt. The abundance of testimonial letters concerning the miracles wrought by the author's "technique" would appear more appropriate in an advertising column.



ONTOGENY AND SUCH AS ISOS.

By Melcherd H. Kutch. *The Christopher Publishing House, Boston.* \$1.50. 7½ x 5½; 119; 1941.

There is very little about ontogeny in this book. Whether Isos is represented the reviewer is unable to say, for he has been unable to locate that word in any dictionary to which he has access.

The forty-two chapters which comprise this work are of unequal weight. Some consist of newspaper clippings about Lina Medina, Robert Wadlow, and the Dionne children, some consist of unorganized material (Lincoln's Gettysburg address is interpolated into an exposition of Egyptian cosmology), and some consist of nothing at all except the caption. It may be desirable to have the accumulated wax removed from one's ears, but why should such medical advice be united with a discussion of the brotherhood of man and the cost of relief?

On the whole the book contains much that is good and original, but "the parts that are good are not original and the parts that are original are not good". Among the latter may be mentioned a few errors in

grammar, diction, and orthography, one of which seems to disclose the author's unfamiliarity with the traditional Negro jargon.

"Juba dis and Juba dat
Juba killed de yaller cat
For to make he wife a Sunday hat,
Juba!"

The subtitle of the work is "A Gift Book". Is this meant to imply that no one will be likely to buy it, and it must therefore be given away? The book is provided with an extensive index. One wonders why.



ADVENTURES WITH A MICROSCOPE.

By Richard Headstrom. Frederick A Stokes Company, New York and Toronto. \$2.00. 8½ x 5½; xxiv + 232; 1941.

The talents of a keen naturalist and successful teacher have gone into the preparation of this fascinating little volume. Although the work is intended primarily for popular consumption among boys and girls of high school age who possess more than a casual interest in the wonders of nature about them, it will undoubtedly find a welcome place on many school reference shelves, and in the hands of leaders of numerous science clubs and nature study groups.

The introduction to the text is a detailed discussion of the structure, use and care of the microscope. Armed thus with the scientist's most powerful weapon, Headstrom leads his readers through some 59 adventures in the microscopic world about us. From one-eyed monsters to bees and bears, mold and worms, roots and silk, the amateur investigator views the proverbial "wonderland". The author's clear and concise directions for collecting and preparing materials for microscopic study, his artistic drawings, and his completely accurate discussions on natural history contribute alike to the excellence of the work. Within these pages, many a boy and girl will undoubtedly hit upon something that will be both a challenge and an inspiration to a life-long interest in nature study.



THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. *A Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, etc., with the Pronunciation, Derivation, and Definition. Nineteenth Edition.*

By W. A. Newman Dorland with the Collaboration of E. C. L. Miller. W. B. Saunders Company, Philadelphia and London. \$7.00, plain; \$7.50, thumb-indexed. 9 x 6; 1647; 1941.

An important volume for the reference shelves of all biological laboratories no matter in what special fields the work may lie. The dictionary first appeared in 1900. Within the last fifteen years it has been increased in size by 300 pages, while in the present edition—the nineteenth—there have been added more than 2,000 words. Many of these new words, of course, come from the rapidly developing science of biochemistry, of nutrition, and allied subjects, but the general biologist will find that his own field has not been neglected.



THE MICROSCOPE. *Seventeenth Edition: Revised.*

By Simon Henry Gage. Comstock Publishing Company, Ithaca, New York. \$4.00. 9 x 6; viii + 617; 1941.

The two previous editions of this classic have already been reviewed in these columns (Vol. 7, p. 348 and Vol. 12, p. 94). The present edition has been expanded and clarified. It is not only a textbook of microscopic technique, but it makes very interesting reading. It contains new chapters dealing with the preparation of objects and one with the history of microscopy. But the great bulk of the work is concerned with the science of optics. It is of course possible to use a microscope without understanding all of the optical principles involved, but the student who does understand them will certainly derive more pleasure and satisfaction from his work, even if indeed he does not accomplish better results.

The index covers 19 pages and the bibliography 15 pages.



THE MIDDLE WEST. *An Approach to Learning and Living through Examination of the Student's Own Environment. A Syllabus.*

By a Committee of the Faculty of Knox College. John S. Swift Company, Chicago. \$3.00 net. 11 x 8½; 1940.

This is a syllabus, with ample space for students' notes, of a full-year course of study conducted by a committee of the faculty of Knox College. The subjects covered include the geology, history, literature, economic structure, sociology, political institutions, education, religion, art, architecture, and music of the region. Reading and essay assignments for the Freshman English course were arranged to fit in with this course and are incorporated in the outline. It should be useful in providing suggestions to school and college administrators and teachers who are interested in introducing a "local interest" course in their schools.

HOW MIRACLES ABOUND.

By Bertha Stevens. The John Day Company, New York. \$2.50. 8½ x 6; 200: 1941.

This work is for the purpose of teaching teachers to teach. Each one of its ten chapters is devoted to the discussion of a commonplace object, and of certain of

its features which are mostly not familiar. This material is arranged in a way designed to interest children, to excite their curiosity, and to make them observant of nature and appreciative of her beauty. The book is well illustrated with both line drawings and photographs, and has numerous quotations from good poetry to increase its aesthetic appeal.

THE QUARTERLY REVIEW of BIOLOGY



DEVELOPMENTAL PROCESSES AND ENERGETICS

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I. INTRODUCTION

AN EMBRYO in its development undergoes a series of complicated changes which proceed automatically towards a well defined goal. To investigate the causes of these changes it is important to learn something of the energy changes involved. There exists considerable information as to the heat production, respiration, etc., of developing embryos. This, with the exception of the more recent work, has been comprehensively covered by Needham (1931) in his treatise on *Chemical Embryology*. In the present article the question of the relation of the energy transformation to the developmental changes will be examined. It will be necessary first to discuss the relation between the various processes that may be assumed to be exhibited by the developing embryo.

The adult form of an organism is a system that is evidently out of equilibrium with its environment. It requires the expenditure of energy to maintain it in a steady state. This process of preserving the form and properties of the adult organism is called maintenance. It may be presumed that the developing embryo, although it is not in a steady state, also exhibits maintenance in addition to processes resulting in increase in amount of living material (growth) and in change of form and composition (differentiation). That maintenance,

growth and differentiation can be distinguished conceptually does not necessarily mean that they are distinct in the embryo. These processes and their components can, however, also be distinguished experimentally in the developing embryo to some extent. An excellent survey of experiments illustrating such separation or dissociation of the various developmental processes has been presented by Needham (1933). Making use of the notion of hierarchical order, Woodger (1930, 1931) has given a logistic analysis of the primary developmental process. Another interesting analysis that may be mentioned is that given by Weiss (1939). Different investigators differ somewhat in their conceptions of these processes. We shall present our own views here without attempting to determine to what extent they differ from or coincide with those of other writers and shall examine some of the evidence concerning dissociability of these processes. Since the cases illustrating dissociation should furnish material for an investigation of the energy requirements, the evidence must be examined rather critically.

II. THE DEVELOPMENTAL PROCESSES AND THEIR SEPARABILITY

1. Maintenance

By maintenance is meant the process of keeping an organism in a steady state. An adult organism in a "resting condition" is considered as exhibiting

maintenance. Also a ripe unfertilized egg would illustrate this. The basal metabolism of an adult organism is ordinarily taken as a measure of the energy requirement for its maintenance, but this has certain implications which will be considered later. The question here is whether or not there is justification for the assumption of maintenance as a distinct process in the developing embryo. This rests on whether or not it is possible to block development in a reversible (non-destructive) manner; that is, in such a manner that there is complete recovery and normal development after the block is removed.

2. Naturally occurring quiescent periods

A reversible blocking of development is exhibited in the normal development of many forms of animals. In mammals, for example, quiescent periods have been reported in the blastocyst stage of the development of the roe-deer, the armadillo and the badger (Hamlett, 1933). In grasshoppers and other insects we find the phenomenon of diapause in which development ceases for a considerable period. This dormant period can be eliminated experimentally (Slifer, 1932). In an atherine fish called the Grunion (*Lewisthes tenuis*), which is found along the coast of Southern California, there is also a dormant stage in development. The eggs of this fish are buried in the moist sand of the beach and develop there up to the time of hatching. They do not hatch out unless they are washed out of the sand. They can be kept in this stage in the sand for at least two weeks and still be capable of hatching when placed in sea water (Clark, 1938). Dormant periods which may extend over years occur in branchiopod Crustaceans (e.g. *Artemia*, *Daphnia*, etc.) and in the rotifers. These forms produce so-called winter eggs which can withstand adverse conditions (drying, cold, etc.) and in which development is blocked at an early stage.

In the various naturally occurring cases the resting phase occurs at a definite stage in development, usually either a very early or a very late stage. It would be desirable to show that development can be reversibly blocked at any stage. The evidence on this point is not as complete and satisfactory as might be desired.

3. Experimental blocking of development

Low temperature, as has long been known, blocks development at any stage. But the different stages give quite different results in regard to

recovery after blocking. It is well known, for example, in hen's eggs that the time of storage at low temperature that will permit subsequent development, decreases very rapidly upon incubation. Also it has not been shown that in these later stages there has been a complete stopping rather than a considerable retardation of development. Only in the case of the unincubated egg has recovery after prolonged and evidently complete blocking by low temperature been demonstrated (Moran, 1925). It is suggestive that the unincubated chick embryo corresponds roughly to the blastocyst stage of mammalian embryos and it is in this stage that normally occurring dormant periods have been described.

Anaerobiosis is another agent that will block the development of animal eggs. But the question of recovery after complete blocking has not been extensively investigated. It is complicated further by the fact that development may occur to some extent under the anaerobic conditions. In the case of the sea-urchin egg this is very slight, but in the frog cleavage may proceed up to an advanced blastula stage (Lennerstand, 1933; Brachet, 1934). Development may also be stopped by such agents as cyanide, carbon monoxide, ether, the urethanes, etc., but the evidence on the resumption of development is again incomplete.

Acidifying the sea-water will block the development of sea-urchin eggs. Resumption of normal development, however, is only possible if the block is of very short duration (Tyler and Scheer, 1937).

Short exposures to very dilute mercuric chloride solutions will block cleavage of sea-urchin eggs (Hoadley, 1930). This block can be reversed according to Rapkine (1931) by immediate transfer to sea water containing cysteine. It was not determined whether reversal is obtained after a prolonged period of blocking or only after a very short period.

Dinitrophenol (and other substituted phenols) will reversibly block the development of eggs of marine animals (Clowes and Krahle, 1934). This appears to be the best agent so far investigated. Development may be resumed after as much as 36 hours of complete cessation (unpublished data). This is as long as the unfertilized egg lives under ordinary conditions.

The fact of the limited length of life of the unfertilized egg, and of the adult organism as well, raises some questions concerning the significance of maintenance to which we shall return. The point to be

made here is that the demonstration of maintenance as a distinct process in the developing embryo does not rest on obtaining an indefinitely long reversible block.

4. Separation of maintenance and growth

The so-called "resting bacteria" (Quastel and Whetham, 1924) have been considered a good example of the separateness of maintenance and growth. Although they do not multiply these organisms are capable of accomplishing many of the enzymatic processes of actively dividing cells. Recovery of the power of reproduction does not occur to any appreciable extent, and on this basis one may not be justified in considering these bacteria alive. A better instance is perhaps that reported by Gegenbaur (1921, cited by Rahn, 1932) in the study of disinfection of bacteria (*Micrococcus pyogenes*) by HgCl_2 . The bacteria after treatment with HgCl_2 are not immediately killed but enter what may be called a dormant stage. They will recover and grow after several hours dormancy when treated with H_2S , whereas washing with water is ineffective in reviving them even after a very short dormant period.

Another line of evidence is found in the nutrition and hormone studies on growing organisms. Most of the work does not quite bear on the point under discussion since the effects studied are usually retardations rather than complete cessation of growth. For example, in the classical case of extirpating the hypophysis (Allen, 1916; Smith, 1916) growth proceeds although at an extremely slow rate.

In experiments on amphibian tadpoles fed on various amino-acids, singly and in combination, in addition to a non-nitrogenous "basal" diet, Guderatsch (1937) presents evidence for the separateness of maintenance, growth and differentiation. On the "basal" diet alone the tadpoles soon die from starvation. The addition of certain amino acids prolongs the life span without appreciable growth and differentiation. Others tended to support growth and others furthered differentiation. The general results are listed in Table 1. Quantitative data are not given as to the extent to which the tadpoles may survive without growing or differentiating, but the results show the possibility of prolonged survival in a static embryonic condition. Similar differential effects on maintenance, growth and differentiation have been described in an extensive series of investigations by Hammett and his

co-workers (1940) who have studied the rôle of amino-acids and nucleic acid components in bud development in the colonial hydroid *Obelia geniculata*.

The best illustration of the separateness of maintenance and growth appears in the work of Osborne and Mendel (1914, 1915). Young rats fed on certain purified proteins such as gliadin, in addition to an adequate non-nitrogenous diet fail to grow but remain healthy and well-formed. They may be kept at constant weight for as long a time as would normally cover their entire growth period and still be capable of resuming growth. The addition of lysine (Osborne and Mendel, 1915) or of cystine (Woods, 1925) to the experimental diet

TABLE 1

Gudernatsch's (1937) classification of amino-acids on the basis of feeding experiments on frog tadpoles

Glycine	} Support maintenance(best)
Alanine		
Leucine		
Aspartic acid		
Glutamic acidmay support maintenance	
	(was toxic)	
Arginine	} Support growth(best)
Lysine		
Cystine		
Phenylalanine	} Support differentiationmay support differentiation
Tyrosine		
Tryptophane		
Histidinemay support differentiation	(was toxic)
Proline		

permits resumption of growth. Work along this line has been greatly advanced in recent years by the use of purified amino-acids instead of incomplete proteins (see review of Rose, 1938).

This work on young mammals distinguishes principally between maintenance and growth since organogenesis is completed long before the start of the experiment.

5. Experiments showing non-dissociability of maintenance

While the above cases tend to show the dissociability of maintenance in the developing organism, there are numerous experiments in which its intimate relation to growth is manifest. It has been shown, for example, that young dogs held at con-

stant weight by restricting the food supply (Aron, 1910, 1911) would die of starvation unless the food were increased sufficiently to permit some gain in weight. Similarly, newborn rats, if maintained at their birth weight, would die in a limited time (Stewart and Jackson, 1920). In young steers, maintained at constant weight, it has been found (Waters, 1908) that the height and length of the animal increases, there being a depletion of fat reserves.

It has been possible also to build up a "growth debt" by keeping young rats at constant weight for varying periods of time (Thompson and Mendel, 1917). Upon return to normal diet the experimental animals grow at an extremely rapid rate and catch up with the controls. This great acceleration of growth rate after a period of inanition was observed earlier in salamanders (Morgulis, 1911). These effects have been re-investigated by Jackson (1936, 1937). He finds that growth repression by under-feeding and by protein deficiency give somewhat different results. Whereas in the latter case the animals practically attain the control size after refeeding, in the former the final weight is significantly (16 per cent in the case of male rats) below the controls. In these experiments the rats were maintained at nearly constant weight for 15 weeks starting just after weaning. There was high mortality and the surviving rats showed, as before, the greatly accelerated growth rate when fully re-fed.

These results do not conflict with those presented in the preceding section (incomplete proteins, etc.). The difference is that here we are dealing with insufficient energy supply along with just sufficient food to maintain constant weight. The result is that some tissues grow at the expense of others and there is an increase in the total requirements which if not met results in starvation death. In the experiments with "incomplete" proteins or with amino-acids, the energy supply is evidently adequate, but one or more constituents essential to the formation of new protoplasm is lacking.

6. *Maintenance and life span*

The life span of organisms and isolated cells in relation to maintenance and growth may next be briefly considered. It is known that favorable environmental factors will prolong to some extent the life span of adult organisms. In the case of the unfertilized egg, which can be considered a resting cell, the life span can be extended by modifying the medium in which it lives. However, only under

certain very special conditions is there any evidence for extremely prolonged survival of organisms and cells.

Certain animal organisms such as the branchiopod crustaceans (brine shrimps, water fleas, etc.) and the rotifers produce "winter eggs" which will survive for considerable periods. The seeds of many plants will survive for years. Spores of unicellular organisms are reported to last decades. Anthrax spores, for example, will survive 20 years. Certain non-spore-forming unicellular organisms will live "indefinitely" if they are rapidly dried. Even such relatively sensitive organisms as meningococcus and gonococcus remain alive and virulent for years under these conditions. Freezing will also keep certain bacteria and other organisms in a stationary viable state, particularly if the process is done rapidly so as to avoid the formation of ice crystals (see Luyet and Gehehio, 1940).

In these cases the systems exist in a relatively solid state in which diffusion processes are reduced to a minimum. The attainment of equilibrium conditions would therefore proceed at an extremely slow rate and it would require a very slight expenditure of energy to maintain the system for an extremely long period of time. Measurements that have been made on the metabolism of organisms under such conditions reveal either a very slight turnover or none at all.

A quite different kind of unlimited survival is evident in the results of tissue culture. The conditions for indefinite survival here involve growth of the tissue. The fibroblasts from the chick heart that have been kept alive since 1912 (Carrel, 1938) are continuously dividing and growing and so must be repeatedly subcultured. This kind of potential immortality of animal tissues was pointed out earlier by L. Loeb (1901) on the basis of long continued transplantation of mammalian tumors (see also Loeb, 1928). The indefinite survival in these cases is essentially the same as that exhibited by unicellular organisms that are repeatedly subcultured. The same sort of thing is illustrated in the case of the long-lived trees, such as the sequoia of California and the baobab of Cape Verde which have survived thousands of years. These organisms remain in the process of growth. Actually most of the tree is considered as dead.

The question as to whether tissues can be maintained outside the animal body for prolonged periods without growth has been examined by Parker (1936). He reports that certain embryonic and

adult tissues can be kept for several months in a functional state. It is this kind of survival which is of particular interest in connection with maintenance. With the exception of this work, it might appear that prolonged survival without growth is only possible by spore formation or some analogous change in state of the cells. The importance of further work along this line cannot be overemphasized, both as concerns the question of unlimited survival as well as the factors that maintain the state of differentiation of the tissues.

7. Maintenance as a repair process

One might consider maintenance as a sort of repair process. On this view it is assumed that there is a continuous disintegration of the protoplasm of the organism. When the building-up processes are sufficient to balance this, we have maintenance. When in excess, we have growth. This view, it would seem, makes the distinction between maintenance and growth a quantitative one. But some of the above evidence and some further considerations indicate qualitative differences. Studies on autolysis of tissues and organisms under sterile conditions (Haehn, 1936; Bradley, 1938) reveal a number of disintegrative changes, of which the hydrolysis of proteins to amino-acids is typical. This auto-digestion simply shows the ability of enzymes to catalyze a reaction in either direction. Now, on the basis of the law of mass action, the addition of any of these amino-acids would serve to displace the equilibrium to the protein side, and thus be effective in maintenance by counteracting the tendency towards hydrolysis of the proteins. For growth, however, all of the amino-acids characteristic of the particular proteins to be synthesized would be required, since the organism always builds up its own characteristic kind of protoplasm.

Some experiments of Voegtlin (1935) on autolyzing muscle, liver and tumor tissue are of interest in this connection. If the material is first kept for two or three hours in a nitrogen atmosphere, there is a rapid decrease in precipitable protein and an increase in amino-acid titre. Upon subsequent exposure for several hours to oxygen, resynthesis of protein occurs with a decrease in the amino-acid concentration. Presumably, although it was not demonstrated in this particular case, oxidations are proceeding under the aerobic conditions and this serves to displace the equilibrium towards the protein side.

Considering maintenance as a repair process is

quite analogous to the generally accepted conception of the equilibrium state of a chemical reaction being that in which the rates of the forward and reverse reactions are equal. So in the maintenance of a living cell the hydrolysis of the proteins may be considered to be proceeding at a rate equal to their rate of synthesis. Where, as is evidently the case with most living cells, the equilibrium conditions are quite different from what would be thermodynamically defined for simple protein-amino acid systems, energy must be supplied to prevent true equilibrium from being attained. Also since most living cells are not isolated systems some of the components are free to diffuse into neighboring cells and into the surroundings of the organism. These components must then be continuously supplied. In cells that are relatively isolated from their environment, or that exist in a relatively dessicated condition, there is very little, if any, energy requirement. In the former case we must assume that the various protoplasmic components approximate conditions of true equilibrium. In the latter we assume that the rate of attainment of equilibrium is exceedingly slow.

One may expect, then, that the maintenance requirements of different kinds of cells will differ under constant external conditions, as will also the requirements for one kind of cell under different external conditions. In a developing embryo the wide variety of cells that are continuously arising will therefore continuously alter the conditions for maintenance, and this is probably one of the difficulties involved in experimentally blocking development (reversibly) at any stage. We may conclude, then, from the above considerations and the evidence available, that there is a distinct maintenance component in the metabolism of the developing embryo.

8. Growth

By growth is meant the conversion of food material into protoplasm. Unfortunately our concepts concerning protoplasm are extremely vague. It is generally recognized that a living cell contains a reserve of non-living material in addition to the "living substance". This reserve may be demonstrated, for example, in inanition experiments. We assume, here, that the material lost up to the point beyond which recovery is no longer possible is simply reserve, while the irreducible minimum remaining in the cell represents the protoplasm. This is admittedly a rather crude way

of regarding protoplasm. For growth studies on such material as unicellular organisms it is, in general, not necessary to distinguish between the protoplasm and the reserve material. The increase in number of cells (of uniform size distribution) may be taken as a direct measure of the synthesis of protoplasm.

In the case of the early development of a multicellular organism, this view of growth presents some practical difficulties. The eggs of most marine invertebrates, for example, absorb no material from the outside (with the exception of water, oxygen and perhaps some minerals) for a considerable period of their development. Here growth, in the sense of increase in mass, does not occur. However, we recognize certain constituents of the egg, such as the yolk, fat, some pigments, etc., as essentially nonprotoplasmic materials. It has been shown, in fact, that such materials can be removed to a large extent without incurring the death of the egg or loss of its ability to develop. During early development these "reserves" gradually disappear and growth in the sense of synthesis of protoplasm evidently occurs. In the case of the large eggs of oviparous animals, we encounter no particular practical difficulties in considering growth in this manner, since a region which is preponderately protoplasmic may be distinguished from one which is chiefly yolk. The embryo arises in the protoplasmic area, and its increase in size at the expense of the yolk is a measure of the conversion of food materials into protoplasm. In the case of oviparous animals with small eggs, the food material is distributed throughout the cytoplasm of the egg, and the embryo is not separated off from this reserve material. By adhering to the definition of growth as synthesis of protoplasm, we evidently introduce difficulties in its experimental determination in the early development of eggs of this type. But this seems preferable to using the evidently fallacious notion that no growth is occurring where there is no increase in mass. One would not think of assuming that a hen's egg, for example, is not growing because there is no increase in total mass up to the time of hatching. Here, of course, we can recognize the embryo as distinct from the yolk at an early stage. To be consistent, then, we must assume that growth occurs in the early development of the small eggs of oviparous animals. The difficulties in quantitative estimation may be compensated by the possibility of utilizing

when necessary the general results of growth studies on various kinds of living things.

9. Storage

Following this line of thought it is also apparent that we must consider a process, called storage, as distinct from growth. This process would represent the accumulation by the cell of reserve food materials. The tremendous enlargement of the young oöcyte as it is transformed into the ripe egg may be considered as being due principally to storage. This process is exhibited particularly in the later stages of development; for example, in the development of the ovary, or in the development of such structures as the fat bodies of insect larvae which are used up during pupation and metamorphosis. Storage may be regarded as a component of the processes of differentiation. But this depends on how differentiation is to be defined.

10. Growth without differentiation

We may consider first some cases illustrating the separateness of growth and differentiation. There is, of course, no point in considering growth without maintenance, since the former *ipso facto* implies the latter. We are interested to know whether at any stage of development growth and differentiation can be dissociated.

An excellent example of growth without differentiation is that of the anidian chick eggs (Dareste, 1882; Grodzinski, 1934). The anidian blastoderm grows considerably with no sign of differentiation. In this example differentiation fails completely to occur right from the start of development. For later stages of development, growth without differentiation may be illustrated by the classical experiments on removing the thyroid of frog tadpoles (Allen, 1916, 1938). As is well known, the animals fail to metamorphose but continue to grow at about the normal rate and attain dimensions beyond the metamorphosis size. There are similar examples in other animals. In insects, Wigglesworth (1936) has shown that implantation of the corpus allatum from third or fourth stage nymphs of *Rhodnius* into fifth stage nymphs would prevent metamorphosis which normally occurs at this stage. The growth and moulting continues, giving a sixth and even a seventh nymphal stage. The corpus allatum seems to restrain differentiation towards the adult form.

Metamorphosis might be considered a special case in that we are dealing with the transition of one kind of fully functional (except generally for reproductive faculties) self-sustaining organism into another form. We might inquire, then, whether before metamorphosis or in the development of a non-metamorphosing species differentiation may be interrupted at any stage without affecting growth.

A difficulty in accomplishing this is apparent in embryos that derive the material for growth from an external source. Suppose, for example, a chick embryo is to be kept in the one somite stage while enlarging to the size attained at hatching. The lack of a proper blood circulation would render the food material unavailable except to those cells adjacent to the yolk. Also oxygen would become unavailable to the internally situated cells as the embryo enlarged. From dimensional considerations this difficulty does not appear avoidable; only abnormal growth or the anarchistic type of growth described by Byerly (1926) seems possible in such a situation.

In embryos that contain the material for growth internally, the difficulty is in recognizing growth as here defined. Suppose, for example, differentiation of a salamander embryo were blocked in the gastrula stage. Continuance of growth would mean increase in the protoplasmic substances (specific proteins, etc.) characteristic of that particular stage, at the expense of the contained yolk materials. Information of this sort is not generally available. It seems reasonable, however, to assume that if cell division continues, in spite of the block to differentiation, protoplasmic synthesis goes on. Using this as a criterion for growth we shall examine some cases of suppressed differentiation.

In salamander embryos it has been shown (Durken, 1935) that ultraviolet radiation of the dorsal lip of the blastopore at the gastrula stage inhibits differentiation, presumably due to inactivation of the organizer. Gastrulation is completed but the neurula stage is not attained. Cell division evidently continues but data are not given from which to decide whether it proceeds beyond the point characteristic of the particular stage.

Interference with the differentiation of specific parts of the embryo without particular injurious effects can be obtained by chemical means (see review of Lehmann, 1937a). The various exam-

ples, however, do not illustrate suppression of differentiation but rather alteration of the type of differentiation. Thus in the classical case of the lithium larvae of sea-urchins (Herbst, 1893; Runnström, 1928) there is a conversion of presumptive ectoderm into endoderm. In the case of the "chorda-lose" salamander embryos (Lehmann, 1937b) the presumptive notochord cells become mesodermal somite cells.

In the numerous defect experiments with which experimental embryology abounds, one might expect to find illustrations of suppressed differentiation. But again it appears in general that altered differentiation results. In the well-known experiment of Lewis (1902-03), for example, extirpation of the optic vesicle results in failure of lens development, but the presumptive lens cells apparently do not remain in the state of differentiation characteristic of the stage of operation but develop into typical ciliated (?) epidermal cells.

Explantation experiments should, it would seem, supply good examples of the failure of parts to differentiate. This type of experiment is the reverse of the defect experiment. In the latter, particular inductors are removed, but inductive action of other parts of the embryo may influence the result; in the former particular parts are removed but inductive action of the culture medium may influence the result. The explantation (interplantation) experiments in amphibia in which parts are transferred to the eye-cavity (Dürkin, 1926; Bautzman, 1929; Kusche, 1929), the body cavity or lymph spaces (Holtfreter, 1929) illustrate such action; a wide variety of tissues developing from the isolated parts. In the more recent experiments of explanting in a neutral salt solution (Holtfreter, 1931, 1933a) the effect of the medium is presumably eliminated. Presumptive medullary plate of the early gastrula cultured in this way forms an irregular mass of atypical epidermal cells, just as does the presumptive epidermis. The few exceptional cases in which some nervous tissue did develop are explained as coming from older embryos. In exogastrulae (Holtfreter, 1933b) failure of the ectoderm to form nervous tissue is also shown. Both in the explants and in the exogastrulae, contact of the ectoderm with an inductor (e.g. chordamesoderm) results in the differentiation of neural structures. If the isolated ectoderm were capable, after being cultured for some time, of reacting to inductors we would be justified in assuming that no

differentiation had occurred while growth, as evidenced by mitosis, continued. But according to Holtfreter (1938, p. 301) the ability of the ectoderm to react decreases with increased time of culturing. The change corresponds roughly to that undergone by the presumptive epidermis in the embryo itself. Thus, at best, we have here only a partial dissociation of growth and differentiation.

A highly interesting example showing independence of growth and differentiation is found in the viviparous medusa, *Chrysaora hysocella* (Teissier, 1929). While the eggs of this animal are all of the same size, the blastulae, gastrulae and planulae are extremely variable. One can find in the same animal planulae that are smaller than many of the gastrulae and gastrulae that are smaller than many of the blastulae. This may be due either to differences in the rate of growth of different eggs, or to differences in the rate of differentiation, or both. In any event it shows that a considerable amount of growth may be obtained without differentiation. Thus planulae may be obtained that vary as much as 300 to 1 in volume, the smallest planulae having only three or four times the volume of the egg. The increase in mass of the embryos is due, of course, to parental nourishment and starts evidently in the blastula stage. Teissier showed that blastulae of radically different size have cells of exactly the same dimensions. Therefore, increase in number of cells parallels the increase in size. Cell division would in this case be an index of growth. Whether it could be generally used as a criterion of growth (as we have defined growth) might possibly be determined on an egg of this type, especially since in the early segmentation stages there is no increase in mass.

A somewhat analogous case is given by the giant and dwarf races of rabbits (Castle and Gregory, 1931). The giant (Flemish) and the dwarf (Polish) races both produce eggs of the same size. The eggs of the former, however, divide much more rapidly, and at identical stages of differentiation the embryos of the larger species are larger. Cell size is the same in both species. This case illustrates an acceleration of growth with a constant rate of differentiation.

We cannot discuss here the numerous cases of genetic size differences in animals that have been studied. But it should be noted that larger size may be attained by prolongation of the growth period as well as by increase in rate of growth. From the evidence presented and many similar

cases that may be found in the literature, it appears that growth without differentiation can occur in embryonic development. The reservation must be made, however, that this has not been demonstrated for very many different stages of development. But this incompleteness may be due to the lack of experiments designed to test this point in particular.

11. Differentiation

The preceding account implies a definition of differentiation as simply those processes not included under what we regard as growth and maintenance. We may then include under differentiation (a) the various form changes (morphogenetic and histogenetic changes) that occur in development, and also (b) the production of the substances characteristic of the various tissues. (a) One may, as is often done, consider the form changes as "directed" growth. D'Arcy W. Thompson (1917), for example, states that "the form of an animal is determined by its specific rate of growth in various directions." This involves a somewhat different definition of growth than here employed. Also, it seems preferable not to use the term growth in this connection unless it is shown that it is impossible for the form changes to occur without increase in protoplasm.

(b) The production of substances characteristic of the various tissues would be included under growth where the particular substances occur in self-multiplicative (self-perpetuating) structures, such as the nucleus, central bodies, mitochondria, etc. It would be included under differentiation in the case of structures that are not self-multiplicative as the fibrillae of various sorts, the cilia, specific granulations, etc. In general it is these non-self-multiplicative structures that characterize the various tissues. This distinction would be valueless if non-self-multiplicative structures were formed only during increase in self-multiplicative structures; that is, during active cell division. Actually, however, the reverse is more generally true; for, as recent evidence from tissue culture work and other sources shows, the visible cellular differentiations appear when cell division has ceased. This will be discussed below.

Although growth can apparently occur without differentiation, it does not follow that the reverse must be true. In discussing this question we must distinguish between what may be termed concomitant growth and antecedent growth.

12. Histogenetic changes

That the visible histogenetic differentiations occur without concomitant growth is evident for most of the tissues of the body, provided that we accept the absence of cell division as a criterion for the absence of growth. The tissue culture work of recent years (see review of Bloom, 1937) shows, in fact, that there is a sort of antagonism between cellular differentiation and growth. Thus actively dividing cells remain "undifferentiated." The cells differentiate only when culture conditions are such that multiplication is inhibited (e.g. delayed growth method of Fischer and Parker). In a recent survey Dawson (1937) points out that contrary to the general view, mitosis may occur in partially or fully differentiated cells without regression of cytoplasmic structures. If increase in the non-self-multiplicative structures occurred simultaneously this would mean an overlapping of cellular differentiation and growth, as we have defined them. Dawson, however, states "The general conclusions of Berrill and Huskins (1936) that there is considerable evidence that cell structures and form can only be developed during the interkinetic phase of the nucleus is probably justified. . . ." It is also well known that in tissue culture, most types of cells transform into fibroblast-like cells or "indifferent" epithelial cells and proliferate as such. We may conclude, then, that cellular differentiation is not only separable from, but generally occurs without concomitant growth, assuming, as before, that mitosis is an index of growth.

The question as to whether cellular differentiation can occur without antecedent growth implies that we have a starting point of zero growth. However, if we exclude the miracle of spontaneous generation, all living cells must have a previous growth history. One might, though, with some justification assume that a ripe unfertilized egg represents the endpoint of one stage of growth and the starting point of another. The same then must be assumed for any cell of the body that has ceased growing (i.e. dividing). The question then is whether such cells (ripe eggs, muscle cells, nerve cells, etc.) can transform into another type without the occurrence of growth. That is, can a cell lose its specific differentiations and elaborate structures characteristic of another type of tissue without going through a growth phase?

The nearest thing to this is perhaps the case described as differentiation without cleavage (Lillie, 1902). Eggs of the marine annelid *Chaetopterus*

were found after treatment with KCl to develop into ciliated trochophore-like structures without having undergone segmentation. But although cytoplasmic division failed to occur nuclear division quite evidently took place resulting in a large number of nuclei or a single large nucleus being present in these atypical larvae. It also has been shown that during the development of such larvae the respiration rises although more slowly than normal (Brachet, 1938; Tyler and Horowitz, 1938) and that there is a synthesis of thymonucleic acid. Growth then in the sense we have been using the term, namely, synthesis of protoplasm, evidently occurs and this case can not be used as an illustration of differentiation without antecedent growth. It does, however, demonstrate strikingly the extent to which the appearance of certain structures and assumption of a definite form is independent of the actual subdivision into separate cells.

13. Morphogenetic changes

We may next consider whether the form changes (morphogenetic changes) can occur independently of growth. If by independent of growth is meant complete absence of antecedent as well as concomitant growth, then evidence on this point is completely lacking with the exception of the case of "differentiation without cleavage," discussed above. Considering only concomitant growth, we know of no cases of the form changes occurring in its absence. In fact, it is generally thought that the morphogenetic changes are directly the result of growth in specific directions, although the term growth is not always used in the same way.

On the assumption that cell division is an index of growth the question is whether a particular form change can occur in the absence of concomitant cell division. Observational evidence on mitotic indices (see recent work of Richards, 1935, for earlier references) of developing embryos tend to show an acceleration of cell division in parts that are undergoing marked form changes. This, however, does not necessarily mean that a particular form change results from increased cell division. The reverse might very well be true or both might result from some common factor. The inadequacy of simply increased mitosis as a causative factor may be illustrated by considering such a form change as gastrulation in an echinoderm blastula. Here, since there is practically no intake of material (except possibly water and some salts) from

the outside there is no increase in mass. Consequently increased cell division in the invaginating region would simply produce smaller cells. But the presence of smaller cells in part of the blastula wall does not necessitate inturning since in the sea-urchin egg by an unequal fourth cleavage there are smaller cells at the antipole during the entire blastula stage. Also removal of these micromeres does not prevent gastrulation (Horstadius, 1928). It is interesting to note too that the only available observations (Schmidt, 1904) show no differences in the rate of cell division in the different regions of the sea-urchin embryo during gastrulation.

It would, of course, be extremely important to determine whether a particular form change such as gastrulation, neurulation, etc., could occur without the normally accompanying cell division. Since such evidence as exists indicates the opposite it may be concluded for the present that morphogenesis is intimately tied up with growth. This does not contradict the previously discussed independence of cellular differentiation and growth, since, as Ranzi (1929, 1931) and others have shown, the histogenetic changes are to a large extent independent of the form changes.

14. *Differential effects on the rates of growth and differentiation*

In the preceding section it was pointed out that there is no evidence of the morphogenetic changes occurring without any growth. There is, however, evidence showing that the rate of differentiation may be accelerated with respect to growth. The precocious metamorphosis that resulted from feeding thyroid to frog tadpoles is considered by Guderatsch (1912, 1929) as demonstrating differentiation without growth. Actually growth, as we use the term, very likely occurs during metamorphosis, the material being supplied by the resorption of certain parts. More strictly, the thyroid feeding advances the time of onset of the metamorphic change. The transformation itself is apparently not speeded up. Whether this, then, should be regarded as an acceleration of differentiation is a debatable question. Certainly there is no evidence that the early stages in the development of the tadpole are speeded up by thyroxine treatment, or by any other agent inducing precocious metamorphosis. As was pointed out in a preceding section it would be better to consider examples from non-metamorphosing forms or in stages of development not including metamorphosis.

A question that arises in connection with the work on metamorphosis is how far the time of onset may be advanced. The evidence shows that very young frog tadpoles may be made to metamorphose, but even the youngest of these are still "fully" developed tadpoles. There is normally, prior to metamorphosis, a considerable period during which growth without any marked form changes occurs, although such cellular differentiation goes on as must accompany the increase in size of the various organs. It would be of interest to know whether metamorphosis can be made to occur before this period. Advancing it sufficiently far would, of course, amount to eliminating it altogether. We would then have direct development from egg to frog, which does in fact normally occur in certain species of amphibia (see Noble, 1931).

Some experiments on chick embryos illustrate a differential acceleration of differentiation with respect to growth. Hoadley (1929) found by transplanting embryonic parts to the chorio-allantoic membrane that the organs which developed were much smaller than those of the intact embryo at comparable stages of differentiation. This was examined particularly in the case of the spinal cord, the mesonephros and the eye. The size of the organ is smaller the earlier the stage at which the transplant is made. Thus, the eye that developed from a transplant from a 20-hour chick was about $\frac{1}{10}$ of the control size while that from a 48-hour chick was $\frac{1}{3}$. Cell size was observed to be the same in the grafts as in the controls. There are, then, fewer cells present in the graft, so cell division was quite evidently retarded. Similarly, Waddington (1932) found that when whole blastoderms are cultivated in vitro, the embryos that develop are much too small for their stage of differentiation. The rate of differentiation was slowed up in comparison with the intact embryo but the rate of growth was retarded considerably more. The previously mentioned rule of an antagonism in tissue culture between growth and cellular differentiation perhaps accounts for these results. But there is also in these two cases a relative acceleration of the form changes as well. So the morphogenetic changes too are to some extent independent of growth.

15. *Brief Summary*

We have attempted in the preceding pages to define the fundamental processes that are generally

assumed in development and examined some naturally occurring and some experimentally produced cases in which the integration of these processes appears to be altered. We may summarize the discussion briefly as follows: (1) there is good evidence for maintenance occurring without growth and differentiation. (2) Maintenance and growth may occur without differentiation. (3) Cellular differentiation occurs without growth. (4) There is no evidence as yet that the form changes can occur without growth but the rates can evidently be differentially altered.

The evidence affords for the present sufficient justification for distinguishing between these conceptually different processes in development.

III. EVIDENCE OF ENERGY REQUIREMENTS

1. *'A priori' considerations*

The processes of differentiation are what characterize the developing embryo in comparison with the adult organism or with a tissue culture of actively growing cells. We are therefore interested in determining the energy requirements for the differentiation processes apart from that for the normally accompanying maintenance and growth processes. This could be rather simply done if the requirements for the maintenance component in the developing embryo were the same as in the adult per unit mass, and that for the growth component the same as in the "fully formed" young. But as was pointed out above this is very likely not the case. In fact different cells of the same organism undoubtedly have different maintenance requirements. It is necessary, then, to approach this problem in some indirect manner. There is, for example, the possibility of utilizing experiments and normally occurring situations such as we have described above, in which the differentiation, growth, or both processes are eliminated in the developing embryo. Very little work has been done along this line. Another possibility is to vary the energy requirements for one of these processes while that for the others is unaltered, or, what is very similar, cases in which the rates are differentially altered could be utilized.

It is, in the first place, important to determine whether energy is actually required for differentiation. It has often been stated, principally on the basis of Meyerhof's (1911) and Shearer's (1922) experiments, that no energy is required. Meyerhof's and Shearer's experiments showed that in

sea-urchin embryos the ratio of heat produced to oxygen consumed was constant throughout development. It was assumed, then, that if energy were required for differentiation, there should be a decrease in the heat evolved per mole of oxygen consumed at times when work was actively being performed. There are several objections that may be raised against this point of view. It may suffice to point out that the heat produced carries no identification of its past history in the embryo. A good part of the energy represented by the heat evolved may very well have been used in producing the form changes before it appeared as heat. What those experiments do show, at least for the limited number of stages examined and within the limits of accuracy of the measurements, is that, if energy is required, it is not stored up in the embryo but appears as heat. This would mean that the form changes in development are of the plastic rather than the elastic type.

In the chick embryo there appears to be the possibility that a small percentage of the energy is stored up in the structure, for Bohr and Hasselbalch (1903) found that there was 4 per cent less heat production than should be obtained from the oxygen consumed and the CO_2 evolved. This may be due, as Needham (1931, p. 964) points out, to experimental error.

If energy is stored up in the structure, it might conceivably reside in the increased surface area. Some calculations of Ellis (1933) and Borsook (1935) show that this would be an extremely small fraction of the energy turnover. Using the value for the surface tension of a water-air interface (72.75 dynes/cm.), which is considerably higher than the values Harvey (1931) and Cole (1932) obtained for the tensions at the surface of marine eggs, they point out that the 4 per cent "organization energy" (3480 calories) of the chick embryo would provide for an increase of 2×10^9 sq. cm. But a chick embryo of 50 c.c. volume and with cells that they assume to average one-tenth the volume of a human red blood cell would have a total cell surface of 2.4×10^6 sq. cm., which is 0.1 per cent of what the doubtful organization energy would provide. These calculations leave out of account entirely the increase in intracellular surface, but it is hardly possible even to guess the magnitudes involved. There is, however, not much point to such calculations unless we can conceive of some way of recovering the supposedly stored up energy. This certainly could not be

done by cytolysis, for example, since what is required is a return to the initial state. A true reversal of development would be necessary in order to settle this question.

We know at present of one instance in which reversal has been obtained but this covers only a very restricted initial period in development. This case is a reversal of fertilization (Tyler and Schultz, 1932) obtained by treating eggs of the echinoid worm, *Urechis*, with acidified sea water within a short time (3 minutes) after insemination. The eggs are caused to return to their initial unfertilized state, although the spermatozoön is not expelled but remains in the egg. That the eggs have actually been reversed is shown by the fact that they can be re-fertilized; they then develop as dispersive eggs. During the reversible period the egg undergoes a change in shape from an indented sphere to a practically perfect sphere, whereby there is a decrease in surface area. The return to the unfertilized condition involves a reversal of this change in shape. We might expect that the decrease in surface area would involve a liberation of energy, and the return to the original condition an absorption of energy. But this would be extremely difficult to demonstrate for the short time interval of the change, especially since the values might be very small in comparison with the total energy turnover. If other and longer periods of development could be reversed we would be in a position to answer not only the question of storage of energy in embryonic structure but also many important problems of development.

The question as to whether or not there is an energy requirement for differentiation does not rest on showing that energy is stored up. In discussing this question we must consider separately the mechanical changes and the chemical changes of differentiation. These correspond respectively to the form changes and to cellular differentiation, although in using these terms it must be kept in mind that the latter involves mechanical changes in the form of the cell and the former must have chemical transformations as a basis. (Huxley's "chemo-differentiation").

2. The chemical changes

When we speak of the energy requirement for a particular chemical change we mean the total energy that must be supplied in order for the reaction to occur. Reactions that proceed spontaneously evidently require no energy. To decide,

then, whether or not the production of the particular substances characteristic of the various tissues requires energy, one would have to determine whether the reactions would proceed spontaneously from the precursors in the concentrations present in the cells. Data on this are lacking, however, in many respects. Not very many of the characteristic tissue substances are known in pure form, and, where the substances and their concentrations and state in the cell are known, the precursors are not. Even the origin of a substance as well known as haemoglobin is obscure. Determinations of equilibrium constants or of the free energies from which the constants could be obtained can hardly be made if the reactions cannot be precisely formulated.

Let us, however, consider the situation in a general way, without distinguishing particularly between cellular differentiation and growth. In the hen's egg it appears that the raw materials are not very different from the materials of the embryo itself (see Needham, 1931, p. 1062). The processes of cellular differentiation and of growth involve the transportation of the raw materials from the yolk to the cells of the embryo. For those raw materials, such as proteins, which are present in the form of large molecules, breakdown into smaller entities (polypeptides or amino-acids) is evidently necessary before they can be absorbed by the cells. We need not consider, at this point, whether or not this breakdown proceeds spontaneously, i.e. with a decrease in free energy. Let us assume that the materials of the embryo have about the same free energy content as the raw materials (which seems reasonable on the basis of the above-mentioned similarity between embryo and yolk materials). If, then, the breakdown processes involve a decrease in free energy the synthetic process will involve an increase and vice versa. Since the sites of breakdown and synthesis are far removed from one another, it is evident that energy liberated by one of the processes is not likely to be utilized by the other. It may be concluded, then, that the overall process of converting the raw materials into embryonic materials (representing both growth and cellular differentiation) very likely requires energy in eggs such as that of the chick. We shall not discuss here the question as to the amounts stored and dissipated, nor the relation to energy supplying mechanisms, coupled reactions, respiration and fermentation.

In eggs of viviparous animals such as mammals, the raw materials are evidently supplied in the form

of smaller entities, the breakdown processes having occurred in the maternal organism. Here, then, it would be necessary to decide whether the synthetic processes require energy. For the synthesis of proteins from amino acids there is no data as to the energy relations. For the synthesis of dipeptides from amino acids in dilute solution energy must be supplied, as recent free energy data show (Huffman, Ellis and Fox, 1936). If, as appears likely, protein synthesis proceeds over this path, and if other synthetic reactions are analogous, we may conclude that the chemical changes of cellular differentiation and growth probably also require energy in this type of egg.

In the small holoblastic eggs of oviparous animals the raw materials are contained intracellularly and there is no evidence that they must be broken down, transported and resynthesized into the materials of the embryo. It is entirely possible that very little change is required to form the materials of the embryo or that the change involves only the breakdown reactions (probably but not necessarily attended by a decrease in free energy) or that energy liberated in breakdown is utilized in synthesis, etc. It would be important then to determine the kinds of chemical changes occurring in this type of egg. From the information available it cannot be decided whether, for example, there is a synthesis of protein from amino-acid during development. If such synthetic processes occur the situation would be analogous to that in eggs of viviparous animals.

In regard to the energy cost of cellular differentiation there is not very much that can as yet be said. The heat production and respiration of developing embryos has, of course, now been determined in a large number of animals (see Needham, 1931, part III, section 4). But as we have seen the values may be attributable to maintenance, growth and the form changes as well as the chemical changes of differentiation. It would be necessary to know the values of the chemical work performed and the free energy change in the energy-supplying reaction in order to state the efficiency. This would be simply the ratio of the former to the latter. The usual methods of determining free energies involves measurements of chemical equilibrium or electrode potentials on well-defined systems. In recent years application of the third law of thermodynamics has led to the determination of free energies by calorimetric measurements of entropies and heat contents (see Parks and Huff-

man, 1932 for application to organic compounds), and this appears to be the most promising method for dealing with substances involved in biological systems.

3. The mechanical changes

For an elastic type of body, the energy required (per unit volume) to produce a given form change characterized by a definite amount of shear, s , would be

$$E = \int_0^s f ds \quad (1)$$

in which f is the applied force (or shearing stress) and is a function of s . Where Hooke's law, $f = Gs$, holds, then

$$E = \frac{1}{2} G s^2 \quad (2)$$

in which G is the shear modulus. For elastic deformations other than simple shear, other parameters would have to be introduced. This energy would, of course, be stored up as elastic potential energy, recoverable as work or heat upon reversal of the form change.

For a fluid type of body the energy required (per unit volume) would again be given by (1). But since here f depends on the rate of shear, ($D = \frac{ds}{dt}$), we may substitute Ddt for ds and

$$E = \int_0^t f D dt \quad (3)$$

In ordinary (Newtonian) liquids

$$f = \eta D \quad (4)$$

in which η is the coefficient of viscosity (or of internal friction) then

$$E = \eta D^2 t \quad (5)$$

This energy would be dissipated immediately as heat and the form change can only be reversed by further expenditure of energy.

Actually the embryo exhibits properties of both elastic and fluid bodies. If it is rapidly compressed and released or stretched and released, it returns to its original shape. But upon prolonged deformation the return is inhibited. Such behavior is characteristic of what are termed plastic bodies. The deformation of a plastic body may be treated in the same way as that of an elastic body with the introduction of a term for what is called relaxation.

Also it might be treated as a fluid body with a certain yield value of the applied force below which no flow occurs. Relaxation effects a decrease in internal stress of the deformed body with time. Assuming simply that in the interval of time, dt , the stress decreases in intensity by dt/R , in which R is a relaxation time constant, we have

$$df = -\frac{f}{R}dt \quad (6)$$

The decrease in internal stress ($-df$) under a constant applied force results in further deformation (increase in amount of shear, s), that is

$$-df = G ds \quad (7)$$

and substituting this in (6) we have

$$Gds = \frac{f}{R}dt \quad \text{or} \quad f = GR \frac{ds}{dt} \quad (8)$$

Writing D , the rate of shear for ds/dt brings out the similarity of this equation to equation (4). In place of the viscosity coefficient, η , there is here the product of the shear modulus, G , and the relaxation time, R . The behavior, then, is that of a liquid with a viscosity equal to GR .

This brief treatment of elastic, fluid and plastic bodies is presented here merely to illustrate the kind of information that is required. Even with homogeneous substances the situation is much more complicated than is represented here (see Love, 1927; Houwink, 1937, or other treatises on elasticity and plasticity). In a heterogeneous system, such as an embryo, with a number of structural elements of different types, the deformation will be controlled by a large number of parameters and the relations would be extremely complex. Possibly some relatively simple measurements of viscosity or of elastic moduli and relaxation or of some other properties might enable us to determine the energy required for a particular form change. At present such direct determination does not seem feasible.

A few words may be said concerning the justification for assuming that the form changes of a developing embryo are of the plastic type. If an embryo is killed by heat or radiation or chemical agents it retains its form. The objection might be raised that the process of killing has altered the material in such a way that elastic stresses are relieved. In that case heat would be expected to be produced equivalent to the loss in elastic potential energy. While no information is available on

the "death heat production" of embryos, measurements on yeast and on erythrocytes (Lepeschkin, 1937) show no very appreciable effect. Also the killing process might just as conceivably allow elastic recovery to occur if the system were one exhibiting "blocked elastic deformation." For example in resins (Houwink, 1934) an increase in temperature is required for recovery to proceed to completion after deformation and similarly in wool (Astbury, 1933) treatment with a chemical agent.

If instead of killing the embryo the energy supplying systems are blocked the form is likewise retained. This may be done by such agents as cyanide, anaerobiosis, iodoacetate, fluoride, etc., which act on the respiratory or fermentation mechanisms. It is possible, however, that other systems take over the energy supplying job in such cases. Other reasons for considering the form changes to be of the plastic type are the failure of recovery of original form after prolonged application of an external force and the constancy of the calorific quotient, mentioned above.

4. The principle of similitude

It has been possible, by indirect means, to demonstrate an energy requirement for differentiation and to elucidate certain problems of development (Tyler 1933-38). This work involves the employment of what is known as the principle of similitude or dimensional analysis. A systematic treatment of the methods of dimensional analysis is given by P. W. Bridgman (1931). Briefer accounts and applications are given by Rayleigh (1896, p. 429 *et seq.*, 1915), Kelvin and Tait (1903, p. 300 *et seq.*), Tolman (1914), Buckingham (1915, 1921) and the *Dictionary of Applied Physics* (1922, vol. I, p. 81 *et seq.*).

We need not, then, go into the details of the method here. The essential features of the principle are that the dimensional formulas of all quantities dealt with in formulating natural laws are expressible as products of powers of the fundamental quantities and that all terms in any equation having a physical significance must have identical dimensions. Tolman (1914) considers the basic postulate as a relativity principle and states it as follows: "The fundamental entities out of which the physical universe is constructed are of such a nature that from them a miniature universe could be constructed exactly similar in every respect to the present universe."

The principle serves not only as a check on any

formula derived either on experimental or theoretical grounds, but can be turned to advantage by providing *a priori* information regarding the forms which the results of any investigation ought to take. It is extremely useful in the preliminary analysis of any proposed problem. It is most extensively employed in model experiments, such as are made in aeronautics, in which it is desired to predict the behavior of a full scale machine or part from measurements made on a small scale model.

According to Pütter (1911), Galileo was evidently the first to employ the general principle for living as well as non-living structures. He showed that there must be a limit to the size of building or animal that could be constructed if the relative proportions of the structure and the kinds of building materials were unaltered. This follows from the difference in the way in which the structural strength and the weight vary with the dimensions. The former increases with the square of a linear dimension, the latter with the cube, so that there is a limit beyond which the structure collapses under its own weight.

Spencer (1898, p. 155) employed this principle in discussing the sizes attained by various animals in relation to their habitat. He plausibly accounts, for example, for the fact that the Condor, which is the largest bird that can fly, weighs only 30 to 40 lb. and that no land animal of the size of the whale exists. Pütter (1911, p. 884 *et seq.*) and D'Arcy W. Thompson (1915, 1916) made extensive use of the principle of similitude in discussions of the growth, the speed, the shape and the metabolism of animals. A recent application of this dimensional reasoning was made by Langmuir (1938) in showing that the often cited figures of 600 to 700 miles per hour for the speed of the deer-fly are not possible. At such speed of flight this insect would have to consume its own weight of food every second, assuming that it has about the same thermodynamic fuel efficiency as man. A more reasonable speed comes out to be about 25 miles per hour.

These examples are presented here simply as illustrations of some applications that have been made of the principle of similitude. The work on dwarf embryos, which will next be discussed, represents, I believe, the first attempt to apply the principle to a biological problem of experimental nature.

5. Dwarf embryos

To determine whether or not there is an energy requirement for differentiation it would, as we have

already suggested, be advantageous to produce embryos in which we might expect the requirements for differentiation to be altered without affecting growth and maintenance. It appeared (Tyler, 1933) that these conditions might be satisfied by dwarf embryos, such as Driesch (1891) first showed can be obtained by separation of the two cells of the two-cell stage of the sea-urchin egg. Since the amount of living material and also the rate of subsequent cleavage are unaltered by separation of the two cells, the two dwarf embryos should have the same maintenance and growth requirements as one whole embryo. The requirements for the form changes of differentiation, however, should be greater in the case of the two dwarf embryos. To show this we make use of the principle of similitude. We wish to determine the ratio of the energy required (work done) in the normal (full-sized) embryo to that in the dwarf embryo when both undergo similar changes in shape. The change in shape that we shall consider is that of gastrulation which is essentially the indentation (invagination) of a hollow sphere, but the results should apply to most of the other form changes that the embryo undergoes.

The dwarf embryo is a small model of the normal embryo. It is not, however, a perfect model. Driesch's (1891, 1900) and Morgan's (1895, 1903) measurements on the dwarf embryos of the sea-urchin showed that, in the blastula and gastrula stages, the surface area (not the volume, as is often supposed) is one half of that of the normal embryo; also that at gastrulation the cells of the dwarf are of normal size, but one-half the normal number. The blastula wall at the time of gastrulation is then of the same thickness in the dwarf as in the normal embryo, which means that it is too thick in proportion to the size of the dwarf.

The relations of the dimensions of the dwarf and normal blastulae are illustrated in Fig. 1. Since the surface area of the dwarf is one-half the normal, then if D is the normal diameter that of the dwarf is $D/\sqrt{2}$. If the dwarf were geometrically similar to the normal its wall thickness should likewise be $d/\sqrt{2}$, where d is the normal wall thickness. A hypothetical dwarf of this wall thickness is illustrated in Fig. 1b. The actual dwarf blastula, of wall thickness d , is represented by Fig. 1c.

We must compare first the normal embryo (Fig. 1a) with the geometrically similar hypothetical dwarf (Fig. 1b). If the production of a deformation characterized by the depth of invagination a

requires the force F in the normal embryo, then by the principle of similitude the similar deformation, $a/\sqrt{2}$, in the hypothetical dwarf will require the force $F/\sqrt{2}$. The work done, or energy required, in the hypothetical dwarf will be one-half that in the normal embryo. Now in proceeding from the hypothetical dwarf of wall thickness $d/\sqrt{2}$

will then be $W/\sqrt{2}$, where W represents the energy required to produce the deformation a in the normal embryo. Two dwarf embryos will then have the energy requirement $W\sqrt{2}$; that is, 1.41 times that of one normal embryo. The actual figures may very likely be quite different depending for one thing on how the forces vary with the wall

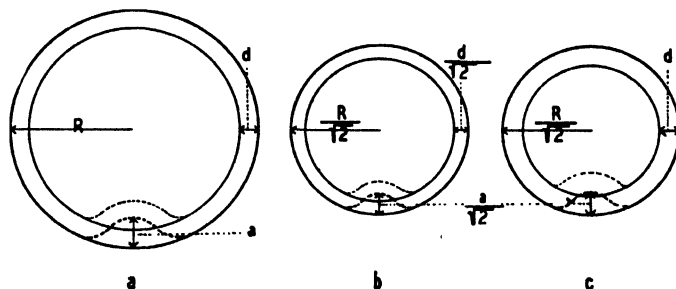


FIG. 1. DIAGRAM SHOWING THE RELATIVE DIMENSIONS AT THE TIME OF GASTRULATION

a, normal embryo; *b*, hypothetical, geometrically similar dwarf embryo; *c*, actual dwarf embryo from an isolated blastomere of the two cell stage. See text for further details.

to the actual dwarf (Fig. 1c) of the original wall thickness d , it is evident that the latter will require a greater force than will the former in order to give a deformation characterized by $a/\sqrt{2}$ in both cases. Just how much greater this force must be will depend on the way in which the force varies with the wall thickness. If we assume that it varies linearly with the first power, then, where F_d is the force required by the actual dwarf,

$$\frac{F_d}{F} = \frac{d}{\sqrt{2}}$$

and $F_d = F$. The work done or energy required in producing the deformation $a/\sqrt{2}$ in the dwarf

thickness, the solution of which is not readily obtained for a hollow sphere. In any event it is evident that there will be a considerable increase in force required in going from the hypothetical dwarf to the actual dwarf.

The expectation, then, is that for corresponding form changes there should be a greater energy requirement in the case of two dwarf embryos than in the case of one normal embryo. On the simplest assumption this increase should amount to 41 per cent. This conclusion was tested experimentally by measurements of the respiration and rate of development of dwarf and normal embryos.

(To be concluded)





CONTRIBUTIONS TO THE PHYSIOLOGY OF FORM GENERATION IN THE DEVELOPMENT OF THE SEA URCHIN

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ALMOST all of our knowledge about the physiology of form generation in ontogeny has been achieved by studies on the eggs of the amphibians and the sea urchin. Although the development of these objects shows certain general features, probably due to common processes in the generation of form, they differ in other essential points. Thus Needham in a review of developmental physiology points out: "Instead of primary and secondary organisers, workers on echinoderm development prefer to speak of a double gradient system. . . ." It therefore seems necessary to the author to give a short survey of the development of this gradient hypothesis and the facts on which it is based.

The first conception of a gradient as put forward by Boveri in 1901, was based upon the differentiation of isolated fragments. Besides morphogenetic criteria for gradients, criteria based on considerations of physiological observations and protoplasmic structure have been put forward. Thus certain regions differ in some respects: (1) sensibility to destroying agents (Child, 1916; Runnström, 1925, 1928); (2) changes in the tendency of the embryonal regions to differentiate after suitable chemical treatment (Runnström, 1928; Lindahl, 1936); (3) distribution of potencies and capability of induction (Hörstadius, 1935). (The term "induction" here used by Hörstadius has a wider meaning than that used for amphibia.) It is a striking fact that all these qualities are graded with a distinct continuity. If we, for instance, speak about a "vegetative organiser", as was formerly done by Hörstadius, it would be quite impossible to state its limits, some of its actions extending—although with diminishing force—all through the vegetal half. Therefore workers on sea urchin development prefer to use the term gradient instead of organizers. As a matter of

fact the conception of a double gradient system is adapted to the problems of determination in the early development of the sea urchin. Probably certain corresponding relations govern amphibian development, at the determination along the egg axis.

That which is essential and new in the gradient hypothesis of Runnström (1928, 1929, 1931) is the *antagonism* between *two* principles existing as gradients along the egg axis, their highest intensity being found at the animal and vegetal poles respectively. This hypothesis was originally founded on two facts: (1) the removal or damaging (by lack of potassium or sulfate ions) of the vegetal region leads to supernormal extension of the most animal differentiation, the apical tuft; (2) the enlargement of the vegetal differentiations, mesenchym and entoderm, caused by treatment with lithium ions, which at that time seemed to be based on an inhibition of the animal material. Later, however, it turned out that this mode of action of the Li^+ -action could not yet be considered as proved. Nevertheless this hypothesis has been confirmed in the most impressive way by the transplantation experiments carried out by Hörstadius (Abstract, 1939).

The action of the vegetal principle finds its expression in two different ways: (1) by an induction of entodermal differentiations; (2) by restraining the tendencies of extension of the most animal differentiation, the ciliated tuft. Thus the vegetal material differs from an organizer in the amphibian development, which only induces a certain differentiation. Without paying attention for the moment to the inductive action of the vegetal materials, we will now turn to the capacity of vegetal parts transplanted into isolated animal halves of restraining the tendency of extension of the animal differentiations. Experiments of Hörstadius show micromere material to be twice as active as macro-

mere material. The same faculty is also present in the vegetative parts of the presumptive ectoderm, though to a much lower degree. Thus the decrease of the vegetal principle is clearly demonstrated. The decrease of the animal principle along the egg axis can in the same manner be demonstrated by the number of micromeres necessary to cause the two most animal discs of cells of the 32-cell stage to differentiate into a normal pluteus. This number is four for the more animal disc and two for the less animal disc.

The tendency of extension of the animal differentiations is the expression of the mentioned antagonism. The enlargement of the entoderm in isolated vegetal halves (Hörstadius, 1939) demonstrates a corresponding, though less striking, tendency of the vegetal principle. The demonstrated earlier fixation of the determination (Runnström, 1928; Hörstadius, 1939) in the vegetal than in the animal egg-half suggests an explanation of the fact that the tendency of extension of the vegetal principle asserts itself to a smaller degree than the animal one. Apart from the inhibiting effect of the animal principle on the tendency of extension of the vegetal one, its organizing capability also shows itself in transplantation experiments. An animal half fused together with an inverted vegetal one forces its polarity to a large extent upon the latter (Hörstadius, 1928).

Besides the antagonism between the animal and vegetal principle which by extreme excess of the one can lead to complete extinction of the other, there is one more phenomenon appearing in isolation and transplantation experiments, obviously of great importance to the spatial realization of the two principles. Removal of the most animal material, which normally differentiates into the apical tuft, enables the less animal material to perform this differentiation. Removal of the skeleton forming material, the most vegetal one, causes the less vegetal material to form the skeleton. The same phenomenon occurs in isolated equatorial fragments, in which the animal part differentiates into more animal structures and the vegetal part into more vegetal ones than either one does in its normal position (Hörstadius, 1935). Obviously the *parts of the embryo containing the two principles in highest intensity exert inhibiting effects, restraining the realization of the same principle in regions of lower intensity* (Lindahl, 1936). This phenomenon is most striking in the development of the isolated presumptive entomesoblast,

where even ectoderm is formed (Hörstadius, 1935). This regularity, which I would like to call "polar dominance" (not to be confused with the "physiological dominance" of Child, which has a much wider meaning) was already recognized in the vegetal region of the embryo by Boveri in 1901. The same phenomenon was later named *Neukonzentration der Gefülle* by Hörstadius (1935), and *Entmischung* by von Ubisch (1936), terms which can only be considered as formal descriptions.

The animal and vegetal principles, the antagonism between the two and the "polar dominance" existing within them are the bases of all regulation along the egg axis. They are also the condition of the so-called *Ganzfaktor* and the harmonious development in the developmental mechanics of the sea urchin egg. Besides these factors the instant of the definite fixation of determination in the different embryonic parts determines the shaping of isolated fragments, as well as their various combinations.

It must be emphasized that the animal and vegetal graded principles have been demonstrated up to the present only in morphological experiments. Consequently they ought to be called "morphogenetic gradients."

The differentiation of an embryo or a fragment depends—as often pointed out by Hörstadius—on the quantitative relation between the two principles. But also their spatial arrangement and the possibilities of influencing each other seem to be of great importance. Thus a stretching of the egg along the egg axis (Lindahl, 1932) or an equatorial constriction (Hörstadius, 1939) causes an enlargement of the apical tuft. The readiest explanation of this phenomenon, as well as of other similar ones, is given by the assumption that the vegetal principle influences the animal by means of a diffusing compound, and the diffusion path being made less favorable by the treatments mentioned (Lindahl, 1936). This does not, however, imply an identification of this hypothetical compound with the vegetal principle itself (Child, 1940).

ON ALTERATIONS OF THE DETERMINATION BY CHEMICAL TREATMENT

Nowadays nobody will deny that the vegetal and animal principles discussed are to be looked upon as the expression of certain metabolic processes (Child, 1940). The discovery of these processes must be one of the next tasks of developmental physiology.

The relation between the animal and vegetal principles can be changed not only by micrurgical methods, but also by destruction of certain regions of the embryo or interference with the metabolic processes upon which the two principles are based. Such a local destruction, caused by the environmental conditions, will chiefly be localized in the vegetal parts and can, for instance, be caused by lack of K^+ -ions (Runnström, 1925), treatment with SCN^- in hypotonic solution (Runnström, 1928) or by a short treatment with weak Hg^+ concentrations (Lindahl, 1936). The changes of the vegetal material caused by lack of SO_4 -ions should also be mentioned here. All these cases show an enlarged ciliated tuft in consequence of a partial or complete deficiency of the vegetal principle.

Far more interesting are the results obtained with complete embryos, which, without being

recognition of such a circumstance, although not always possible, is of great importance, since otherwise false conclusions are likely to be drawn.) It may be concluded that the treatment chiefly inhibits or advances some metabolic processes of morphogenetic importance, leaving other vital processes undisturbed. The interference causing vegetalization which has been most investigated is the treatment of the fertilized egg with lithium ions according to Herbst. An animalization without destruction of vegetal embryo parts can be obtained by treating the unfertilized egg with sulfocyanide or iodide in the absence of calcium as first performed by the author (1933).

The similarity between the morphological forms which were obtained on the one hand by Li^+ treatment and animalizing treatment and on the other by micrurgical methods (Figs. 2-3) is of great

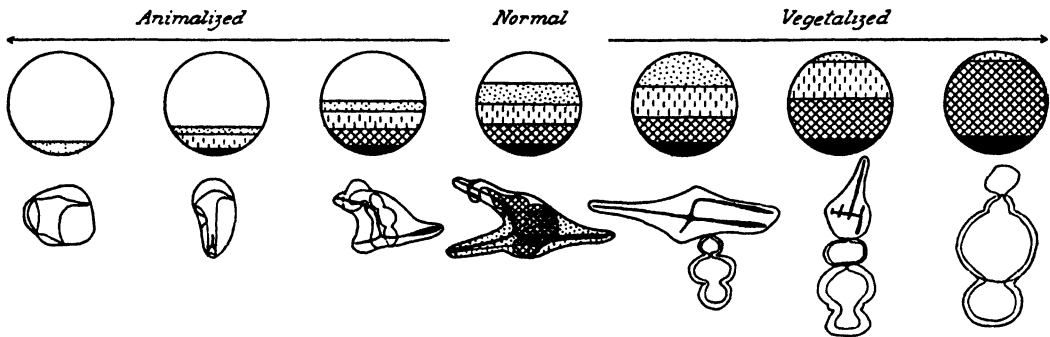


FIG. 1. DIAGRAM OF THE DISPLACEMENT OF ORGAN LIMITS IN EMBRYOS ANIMALIZED BY TREATMENT BEFORE FERTILIZATION AND VEGETALIZED BY Li^+ TREATMENT

In the middle the presumptive meaning of the material in the normal development according to Hörstadius 1935. By aid of this scheme the distribution of the presumptive organs in the different cases of animalization and vegetalization has been drawn. Note the rotation of the plane of the oral field accompanying vegetalization.

locally destroyed, become animalized or vegetalized by treatment with certain chemical agents. That is, they differentiate in a more vegetal or more animal way than normally. The terms "animalized" and "vegetalized" are used to describe briefly displacements of the organ limits (Fig. 1) in vegetal or animal direction. They do not coincide with "endodermization" or "ectodermization", since vegetalization does not necessarily include endodermization or animalization ectodermization. Being treated with a suitable dose the embryos will be able to live and differentiate. (A great difficulty in judging the developmental results in such experiments depends on the fact that the chemical treatment not only causes the intended changes in morphogenetic harmony, but also inhibits more or less the normal differentiation, without causing destruction. The

importance in the analysis of the changes in the metabolism caused by the treatments in question. This concordance justifies the conclusion that the Li^+ treatment changes the relation between the two principles in such a way that the animal principle becomes weaker or the vegetal stronger. A combination of these two possibilities might also be considered. In the animalized embryos the treatment correspondingly either weakens the vegetal or strengthens the animal principle.

Metabolism and determination

Since the sea urchin embryo is a pronounced aerobic organism, it can be expected that a great number of metabolic processes are directly or indirectly coupled with oxygen consumption. Thus a diminution or a reinforcement of certain metabolic processes may be observed in corre-

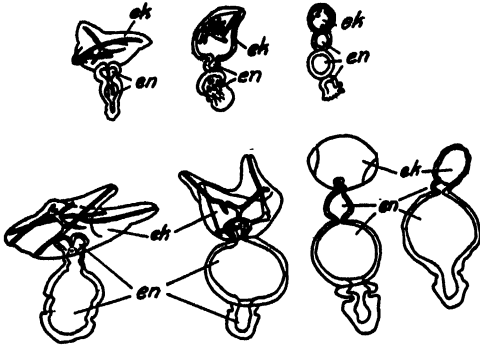


FIG. 2. *PARACENTROTUS LIVIDUS*, EMBRYOS OF VEGETAL TYPE

Upper row obtained by cutting down the animal material (from Hörstadius, 1935); lower row by lithium ion treatment (from Lindahl and Öhman, 1938). *ek* ectoderm; *en* endoderm.

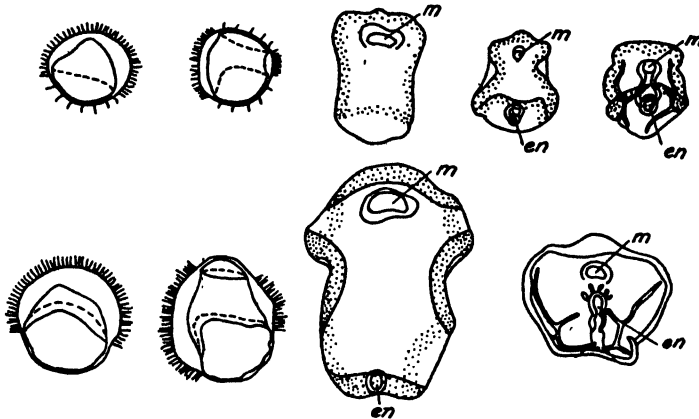


FIG. 3. *PARACENTROTUS LIVIDUS*, EMBRYOS OF ANIMAL TYPE

Upper row obtained by cutting down the vegetal material (from Hörstadius, 1935 and 1936); lower row by animalizing treatment before fertilization (from Lindahl, 1936), *en* endoderm; *m* stomodaeum.

sponding changes in oxygen consumption, and measurements of the respiration might give some orientation about the changes caused in the metabolism.

[Editorial note: At this point in Dr. Lindahl's manuscript a page number is missing. Since it is impossible to communicate with the author to ascertain whether there has been a misnumbering of the pages or whether a page has been lost in transit, the paper is being published in the form in which it has reached the Office of the Editor.]

The changes of normal respiration during development

The respiration of the developing normal sea urchin egg was first investigated by Warburg (1915). He showed that the rate of oxygen

consumption after the sudden rise at fertilization continuously increases during the first 24 hours of development. "There is no maximum, no S-shaped curve and no 'rhythmic' respiration." Later, more detailed researches have revealed somewhat different facts. Thus the respiration during the first 6 cleavages increases according to an exponential function of time (Gray, 1927; Lindahl and Öhman, 1938). This increase gradually ceases and the oxygen consumption remains constant from two to two and a half hours (22.0°C). During this first period of development, lasting till shortly before the migration of the primary mesenchyme, the curve of respiration is S-shaped (Fig. 4). A further increase of respiration which begins suddenly, constitutes the limit between

this and the following period of development, which lasts till the end of gastrulation (Lindahl, 1940). Characteristic for this second period is a constant increase in respiration, the migration of mesenchyme and gastrulation. During the third period of development the oxygen consumption still rises but much more slowly than earlier. At this time the differentiation of tissues and the formation of body shape is taking place. This period is arbitrarily considered to end with the breaking through of the mouth. The tissue differentiation and the formation of the body shape are far from being finished at this moment, but as the metabolism later on does not depend merely on materials stored in the egg, investigations of the metabolism in later stages are of less interest (Lindahl, 1940). A survey of the behavior of

normal respiration during these three periods of development is given in Fig. 5.

On the action of sulfate ion deficiency

At the end of the last century Herbst found that sulfate ions are necessary for the normal development of the sea urchin egg and that they are of importance only in the late blastula and later stages. Lack of SO_4^{--} leads especially to inhibition of the vegetal parts of the embryo. The entodermal cells are opaque and yellowish and do not stretch themselves normally; thus the entodermal wall remains too thick and often not subdivided. The primary mesenchyme does not, as normally, arrange itself into the well-known skeleton-forming ring, but remains stored in the neighborhood of the intestine. This may be accounted for by the inhibition of factors in the mesenchyme cells or in

and structural disturbances go hand-in-hand with a slight reduction of oxygen consumption (Lindahl, 1935), which appears simultaneously with the need of SO_4^{--} and thus earlier than the visible inhibitory alterations.

The rôle of the SO_4^{--} in the metabolism of the developing sea urchin egg is still unknown. It has, however, been shown that a culture in SO_4^{--} -free sea water gives off more differentiation-inhibiting matter to the medium than does a culture in normal sea water (Lindahl and Stordal, 1937). To test this, the larvae were filtered away, the sea water completed and used as medium for freshly fertilized eggs. The formation of the inhibiting substance in the absence of SO_4^{--} could be demonstrated still better after extraction of the whole cultures with ethyl ether (unpublished experi-

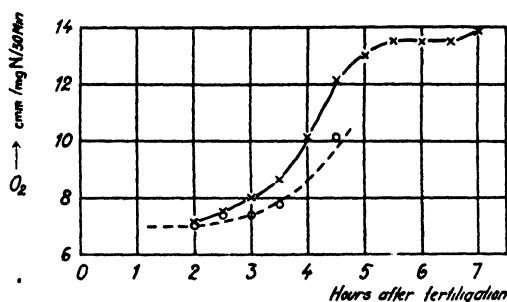


FIG. 4. RESPIRATION OF *PARACENTROTUS LIVIDUS* EGGS AT 26.0°C AS A FUNCTION OF TIME

Solid line = normal respiration; broken line = respiration in 0.081 mol LiCl (from Lindahl, 1939).

the ectoderm, which direct their movements. The region covered by the apical tuft extends itself and the limit between entoderm and ectoderm is shifted toward the vegetal pole. The bilateral organization is more or less suppressed. In extreme cases the embryos may become radially symmetrical.

Though these experiments belong to those which have led to the conception of the antagonistic principles, later research in this field has not brought the solution of the physiological problems of determination nearer, the lack of SO_4^{--} not exerting an action until the determining processes are to a great extent already passed. Nevertheless the localization of certain metabolic processes has been demonstrated in this way.

The animalization which takes place here differs in many essential respects from that caused by treatment of the unfertilized egg. The inhibitions

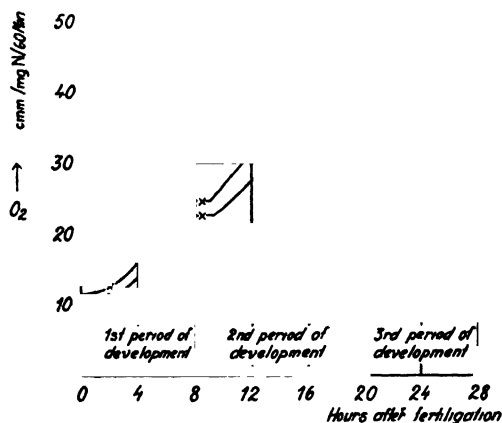


FIG. 5. CHANGE IN RESPIRATION DURING DEVELOPMENT OF THE EGGS OF TWO DIFFERENT FEMALES. *PARACENTROTUS LIVIDUS*

T = 22.0° (from Lindahl, 1939)

ments of the author). As in many other tissues and organisms, a phenosulfatase has also been demonstrated in the sea urchin egg (Lindahl, 1936). Thus there is reason to assume, that SO_4^{--} is needed for the detoxication of intermediary compounds containing cyclical hydroxyl groups. Whether these poisonous compounds are formed in connection with protein metabolism, as assumed for mammals, or with other processes, still remains a problem. Intermediary products in the formation of the pigment echinochrome, which, according to recent research (Kuhn and Wallonfels, 1939), is a naphthoquinone derivative, may also be thought of. Remarkable is the simultaneous commencement of the need of SO_4^{--} and of the increase in respiration just before the migration of the skele-

ton-forming cells. The fact that the vegetal region of the embryo—the chief seat of the formation of toxic compounds in absence of SO_4^{--} —acquires a much stronger power of reducing redox indicators just at this moment, suggests that new metabolic processes are beginning here.

The general features of the disturbances caused by lack of SO_4^{--} demonstrates a localization of the metabolic processes giving rise to the need for SO_4^{--} in the vegetal regions of the embryo. Further information has been obtained by keeping isolated animal and vegetal halves in an SO_4^{--} -free medium (Lindahl and Stordal, 1937). The animal halves behave just as they would in normal sea water and are thus not able to form the toxic products. This statement can, however, not be extended to the animal half in its normal connection. Nevertheless it may be concluded, that the toxic compounds are formed neither in the normal nor in the enlarged apical tuft. That enlargement of this structure is the same in the isolated animal half in SO_4^{--} -free as in normal sea water shows that the reactions controlling this process must have already come to an end, before the formation of the toxic compounds starts. Thus this formation appears with lack of SO_4^{--} , when the animalization in the isolated animal halves is restrained by treatment with a weak Li^+ -concentration (Lindahl and Stordal, 1937). As entoderm still is missing in such cases, they demonstrate that the toxic compounds are also formed in the vegetal ectoderm, though to a smaller extent. The same is suggested by results on entoderm-free embryos, obtained by treatment prior to fertilization. The stretching of the cells in the oral field appears to be especially influenced here, thus suggesting a difference between the dorsal and ventral sides with respect to these metabolic processes.

Isolated vegetal halves in SO_4^{--} -free sea water are still more affected than the corresponding material in normal connection with the animal half (Lindahl and Stordal, 1937). The best reason for this is, that the vegetal half, according to experiments of Hörstadius (1936), has more vegetal character when isolated than under normal conditions. Other explanations, taking into account diffusion of the toxic compounds into the animal half, are also possible. By appropriate treatment with Li^+ , isolated animal halves may be brought to form entoderm (v. Ubisch, 1925). This entoderm in lack of SO_4^{--} behaves just as the normal entoderm of an entire embryo (Lindahl and Stordal, 1937). From this we may conclude, that the

metabolic processes leading to these toxic intermediary products are not confined to a certain material but to a certain determination and differentiation. Consequently these reactions are of no importance in the origination of the vegetal principle but are dependent on the latter and coincide largely with its extension. This is supported by the fact that the production of toxic compounds in lack of SO_4^{--} -ions is initiated at a much later stage than that at which the morphogenetic actions of the vegetal principle may be detected in transplantation experiments.

The action of lithium ions on metabolism, protoplasmic structure, and morphology

Since determination is fixed progressively during the twelfth to sixteenth hour of development (Hörstadius, 1936) and a vegetalization is only obtained by lithium treatment in earlier stages, interest has been concentrated on the metabolic processes of the first section of development. Brought into an egg suspension during the period of the exponential increase of respiration, Li^+ produces an inhibition of the further increase without decreasing the already existing respiration. The quantitative relation between the Li^+ concentration and the inhibition suggests a reaction between Li^+ and an activator in the embryo following the law of mass action (Lindahl, 1936). The similar inhibition of fermentation and respiration in yeast cells by Li^+ as well as the inhibition of the dehydrogenation of hexosemono- and hexosediphosphoric acids with broken eggs as enzyme material and methylene blue as acceptor (Lindahl, 1936), or in the presence of pyocyanine and oxygen as acceptor (Lindahl and Öhman, 1938), made it tempting to think that even in the living sea urchin embryo we are dealing with an inhibition of a carbohydrate oxidation.

To demonstrate the exponential increase of the respiration, Gray (1927) has already made the assumption that the respiration during cleavage consists of two parts, one constant and one increasing. The earlier measurements of respiration in Li^+ -cultures apparently confirming this, it was attempted to support this idea by other facts. It was shown (Lindahl and Öhman, 1938) that the absolute activation of respiration by pyocyanine is the same shortly after fertilization and 9 hours later, though respiration has been doubled in the meantime. Thus the action of the pyocyanine seems not to affect that part of the respiration which has arisen between the two stages, but only

that existing shortly after fertilization. This will remain constant until the 9-hour stage and it later also begins to rise. The recent determinations of the respiratory quotient referred to below are in harmony with these results.

The specific inhibitors of carbohydrate breakdown offer a further possibility of penetrating into these problems, their action possibly being limited to the increasing part of the respiration, since carbohydrates would presumably be the substrates of this part. Monoiodoacetic acid amide does, however, not only suppress the building up of the increasing part of respiration, but inhibits also the respiration already present shortly after fertilization. (Lindahl and Öhman, 1937). Glyceric aldehyde, the action of which on the glycolysis of the chick embryo has been intensively studied by Needham and his coworkers, inhibits principally the further increase of respiration when brought into the suspension immediately after fertilization, leaving unchanged the respiration already present (Lindahl, 1939). Later unpublished experiments of the author show, however, that higher concentrations in the eggs of some females inhibit even the constant part of respiration, not only depressing the further increase as does Li^+ . Characteristic for this action is, however, a certain lag, suggesting secondary reactions at work. This lack of specificity of the action of the glyceric aldehyde together with the heavy destruction of the embryos already brought about by weak concentrations, which inhibit the respiration only to a very small extent, may perhaps be accounted for by a reaction with amino groups. According to Lehmann and Needham (1938) a nonphosphorylating mechanism of glycolysis may be distinguished from a phosphorylating one by means of the monomeric and dimeric forms of glyceric aldehyde. The respiration of the sea urchin embryo is equally affected by the two forms (Lindahl, 1940).

The experiments with "specific" inhibitors of carbohydrate breakdown have so far not contributed to the elucidation of the rôle played by carbohydrates in sea urchin development. It seemed difficult, besides, to combine the idea of an increasing carbohydrate oxidation existing in addition to a constant one of another kind with an RQ of 0.90 in fertilized eggs. This value was first determined by Warburg (1915) and has later been confirmed by several authors (Lindahl, 1936). All these determinations are performed with the three-manometer method of Warburg. In unpublished experiments of the author on the RQ

during development of the sea urchin egg the same method was used and the fact established, that the pH of the cell suspension is lowered in the vessel, where the carbon dioxide formed is not absorbed. An equal respiration in the two vessels provided with KOH and H_2SO_4 respectively being the basis of the determination of RQ, this condition can hardly be recognized as fulfilled, when the pH in one vessel is lowered. So a modification of the method of Meyerhof and Schmit was planned and preliminary experiments carried out by my coworker Öhman (1940). In the 1-2 hour stage, the RQ was found to be 0.73 ± 0.01 , in the 7-8 hour stage 0.85 ± 0.01 . Accordingly fat seems to be the chief substrate burned shortly after fertilization. A calculation of RQ of the part of respiration, arising between these two stages, assuming that the fat oxidation remains unchanged, reveals a value of 1.00. In fact this part of respiration appears to be an *oxidative carbohydrate breakdown*. The analysis of total carbohydrate and fat (Ephrussi and Rapkine, 1928; Hayes, 1938) do not contradict this interpretation. The data of Hayes present a constant decrease in total fat during the second to ninth hour of development. However these determinations seem to be impaired by great errors.

As long as the respiration increases exponentially, Li^+ obviously acts on the metabolism in a *fairly specific way*. Added to the suspension shortly after this increase has ceased, it *inhibits the respiration in another way* (Lindahl, 1939). In this stage Li^+ inhibits not only the further increase of respiration but also the existing respiration. This inhibition does not reach its maximal value shortly after the addition of Li^+ as in earlier stages, but continues to increase. Furthermore, the inhibition of a certain Li^+ concentration is independent of the temperature during the exponential increase of respiration (Lindahl and Öhman, 1937), while the late inhibition is greater at higher than at lower temperatures (Lindahl, 1939). The embryos show a much more pronounced general sensitivity to Li^+ in these later stages than in earlier ones, culminating in destruction and death. It is, however, easy to suggest a causal connection between the changes in the colloidal structure of the protoplasm, caused by Li^+ (Runnström, 1928, 1935) and more marked in the later stages, on the one hand, and the late inhibition of respiration and the general sensitivity of these stages on the other. Certainly a coarsening of the protoplasmic structure by the action of Li^+ could be demon-

strated in earlier stages (Runnström, 1928; Lindahl, 1936). That this coarsening does not appear to determine the inhibition of respiration in earlier stages may be explained by the protoplasmic colloids being considerably less sensitive in these stages. Further the protoplasmic structure does not play the rôle of a limiting factor, the respiration already being depressed by the specific action.

Now we must turn to the question whether there is any causal dependence between the inhibition of metabolism and the vegetalization caused by Li^+ or whether these two actions are to be looked upon as parallel phenomena. The first mentioned possibility would mean that the animal principle is connected directly or indirectly with the metabolic processes which are inhibited by Li^+ . In favor of this may be cited the observation that eggs, the respiration of which is less inhibited by Li^+ , will also be less vegetalized than those in which respiration is more inhibited. However, a much better argument may be based on the following facts: Li^+ inhibits reversibly the exponential increase of respiration. A short treatment thus causes a deficiency in metabolism, the amount of which depends on the duration of the treatment, the steepness of the respiration curve during the period of treatment, and the Li^+ concentration. Treatment during short equal periods of time with the same concentration of Li^+ would thus cause deficiencies about proportional to the increase of respiration during the different periods. Were the vegetalization possibly caused by the deficiency in question, it too should vary in the same way. This is in fact the case (Lindahl, 1940). If embryos are treated in 3-hour periods (developmental temperature 22°C) from fertilization, then those treated during the first period show a weak, those during the second period a strong, and those in the third period again a weak vegetalization. Compare with this the S-shaped form of the respiration curve in Figs. 4-5. Up to 9 hours after fertilization a short treatment thus causes a vegetalization which is weak or strong according to whether the curve of normal respiration is more or less steep during the treatment. This result strengthens the hypothesis, that *a causal relation exists between the part of respiration inhibited by Li^+ and the animal principle*. It does not, however, exclude the possibility that the increasing respiration and the metabolic processes conditioning the animal principle run parallel. The latter would mean that the processes which constitute

the basis of the increase of respiration and the animal principle, are enacted simultaneously and behave similarly towards Li^+ .

After 9 hours from the time of fertilization Li^+ treatment of short duration causes a very weak vegetalization or none at all. (Lindahl, 1940). Thus the inhibition of respiration induced by Li^+ in later stages has no direct relation to vegetalization (Lindahl, 1940). If, however, the treatment is started in earlier stages and extended over the 12-hour stage, then it will exercise a stronger vegetalization the longer it is continued (Hörstadius, 1936; Lindahl, 1940). The treatment in earlier stages thus enables Li^+ to exercise a vegetalizing action in the later ones. This must signify that the fixation of the determination is delayed by the earlier Li^+ treatment. Under these conditions either the same action of Li^+ may be realized in the later stages as in the earlier ones, or Li^+ exerts here another influence, which directly or indirectly leads to a stronger effect of the earlier intervention in the metabolism.

It has often been attempted to gain insight into the mechanism of the morphological action of Li^+ by combining the Li^+ treatment with other agents. Thus elevation of the K^+ -concentration of the sea water weakens the vegetalizing action of Li^+ (Runnström, 1928; Lindahl, 1936). This fact is, however, difficult to interpret, because an elevation of the K^+ -concentration by itself may lead to an enlargement of the apical tuft and consequently to an animalization, which apparently is realized by means of a weak injury of the vegetal material. Nevertheless, measurements show the respiration to be increased by the elevated K^+ -concentration (Lindahl, 1936). In combination with Li^+ the depression caused by this ion is thus levelled by action of the higher K^+ -concentration. A close study of the behavior of the two parts of respiration would in this case be rather difficult to carry out.

The combination of Li^+ -treatment with different agents inhibiting the electron transfer in the respiratory mechanism has been intensively studied. Carbon monoxide (mixed with oxygen) (Runnström, 1933) as well as KCN (Lindahl, 1936) and partial anaerobiosis (Lindahl, 1940) strengthen the vegetalizing action of Li^+ . In the absence of Li^+ only CO causes a vegetalization (Runnström, 1928; Hörstadius and Strömberg, 1940), but it is said to produce an animalization in entire eggs as well. The interesting result (Hörstadius and Strömberg) that CO treatment

causes an animalization in animal halves and vegetalization in vegetal ones suggests an unspecific action being in play. The assumption that CO delays the fixation of the determination, thus giving the predominant principle in the two separated halves a chance of carrying itself through, offers a possibility of explanation.

The equal action of the two respiratory poisons and the partial anaerobiosis when combined with Li^+ shows that we are hardly dealing with a specific quality of the two poisons. The oxidation-reduction state of the cellular components is changed in the direction of being more reduced by the depression of electron transfer. It is thus possible that the substances on which Li^+ acts more or less directly are more influenced by Li^+ when in a more reduced state (Runnström and Thörnblom, 1936). Again, the depression of the electron transfer undoubtedly leads to disturbances of the protoplasmic structure caused either by deficient supply of energy or by accumulation of acid intermediary products. Combining Li^+ treatment with the action of weak organic acids strengthens, however, the vegetalization (Lindahl, 1940). Thus the strengthening caused by depression of respiration may as well be referred to an accumulation of acid intermediary products as to changes in the oxidation-reduction state of certain systems in the cells. For the time being we may tentatively make the coarsening of the protoplasmic structure, which is common to the depression of oxygen transfer as well as the action of acids, responsible for the strengthening of the vegetalization by Li^+ . This would trace an action of different agents back to one ground-phenomenon and would eventually even apply to the action of Li^+ -treatment extended over the 12-hour stage.

There are many descriptions in the literature of exogastrulae obtained by the most different means and classed with embryos modified by Li^+ treatment. Nowadays it must be considered proved, that exogastrulation can appear as a consequence of vegetalization as well as of interventions into the gastrulation mechanism. In the latter case, the embryos are perfectly normally proportioned. The *exogastrula* is by no means identical with the *vegetalized* embryo. Detailed figures and statements prove the existence of vegetalized cases obtained with other agents than Li^+ , including such different treatments as carbon monoxide, auxin, janus green and crowding. Thus Li^+ does not act specifically in the sense that it is the only agent causing vegetalization (Child, 1940). The

action is, however, so far specific that Li^+ inhibits certain metabolic processes, leaving others relatively unaffected. In this respect an agreement with other vegetalizing agents is to be expected.

If the animal principle is connected with some kind of carbohydrate breakdown, as has been shown to be probable, it would be possible to produce a vegetalization with the aid of compounds which selectively inhibit carbohydrate breakdown. Experiments of this kind, however, turned out negatively (Lindahl, 1940; Needham and Needham, 1940). This may depend on the fact that the inhibitors used—monoiodoacetic acid, glyceric aldehyde, phloridzin—not only inhibit the carbohydrate breakdown, but also other vital reactions, this being obvious from measurements of respiration as well as from destruction of the embryos (Lindahl, 1940). The same point of view may even serve as an explanation for the rather contradictory results obtained by Hörstadius and Strömberg (1940). They found monoiodoacetate to cause an animalization in entire eggs and a vegetalization in animal halves. Treatment with phloridzin led in entire eggs to animalization, in isolated animal halves, on the other hand, to animalization as well as to vegetalization. In entire eggs treated with this compound before fertilization, the author obtained a vegetalization (Lindahl, 1940).

Animalization by treatment before fertilization and its mechanism

Sulfocyanide and, in the second place, iodide ions have shown themselves to be very active in causing animalization after treatment of unfertilized eggs. Also other ions such as SO_4^{--} , Br^+ , tartrate, Li^+ are able to bring about animalization in the same way, being, however, less efficient. In this rank belongs probably also an unknown compound, contained as an impurity in a KCl-preparation from Schering-Kahlbaum (pro analysi). It had the same action as the above-mentioned ions and could be removed by recrystallization (Lindahl and Öhman, 1938). As the treatment lasts several hours, it is necessary to eliminate those processes which lead to "overripeness" of the eggs and counteract the animalization. Since these reactions are bound to the presence of Ca^{++} (Lindahl, 1936; Schechter, 1937), the treatment is performed in Ca^{++} -free sea water. This is, however, by no means a necessary condition, but makes the method more reliable.

It is obvious that the action in question is not a

specific one since it is brought about by such different ions. Moreover the ions create certain conditions in the cell enabling specific reactions to take place. According to this, the animalization resulting in some cases from a treatment with Ca^{++} -free sea water alone (Lindahl, 1936) is not very surprising. Certainly we are dealing with some kind of impurity in the chemicals used for the artificial Ca^{++} -free sea water or in the vessels employed, which causes the same kind of alteration in the egg as the ions mentioned above.

The oxygen consumption during the treatment has proved to be of decisive importance. If the treatment is carried out under an oxygen pressure of 2 per cent or less, in the dark in an atmosphere of 5 per cent O_2 + 95 per cent CO or in $6 \cdot 10^{-5}$ mol KCN, the animalization fails to appear (Lindahl, 1936). In all these cases the respiration of the

with such a reaction. Where these oxidations come in, is still completely unknown. Attempts to measure the respiration during an animalizing treatment have never succeeded, because the animalization of the eggs always fails to appear when simultaneous measurements of the respiration are made. Probably certain very labile structural conditions in the cell, which are disturbed by shaking during measurement of respiration, play an important rôle in the processes leading to animalization.

Measurements of respiration on animalized embryos during the exponential increase of respiration show striking divergences from the state of the normal embryo (Lindahl, 1936). One of these concerns the susceptibility of the respiration to Li^+ , which has much increased. Thus certain metabolic systems are altered by the treatment. An interpretation of these facts is not yet possible, nor is it possible to decide whether the treatment primarily causes a weakening of the vegetal or a strengthening of the animal principle.

When the animalization has proceeded so far that all vegetal organs have disappeared, one would expect further progress of this process to be manifested in a greater and greater increase of the apical tuft and the ciliated band at the expense of the lower epithelium. Instead we find (Fig. 6), that a new tuft takes the place of the skeleton-forming cells at the vegetal pole. That we are here indeed dealing with a new physiologically functioning animal pole, may be concluded from experiments in which eggs animalized by treatment before fertilization are exposed to the action of Li^+ . In embryos which have been moderately animalized the vegetal differentiations will now appear and nearly normal or slightly vegetalized embryos develop. This is also the case in embryos which should have differentiated two apical tufts. However, the mesenchyme and the entoderm are not, as in the normal egg, formed from the most vegetal material, which here gives rise to ectoderm, but from the material located just on the vegetal side of the egg equator (Fig. 7). Consequently, without any displacement of material, an inversion of the polarity has taken place in the vegetal third of the embryo. At present this phenomenon is most easily explained by aid of the "polar dominance". At the moment during the animalization, at which the vegetal principle has been totally suppressed, the animal principle, in very low intensity, holds the vegetal region of the egg. Because of the great distance, the most vegetal

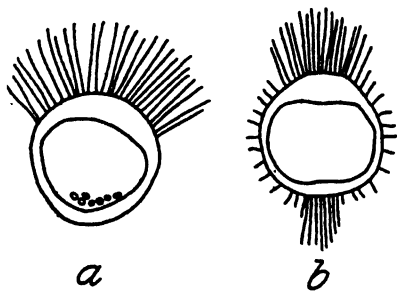


FIG. 6. EMBRYOS OF *PARACENTROTUS LIVIDUS* ANIMALIZED BY TREATMENT BEFORE FERTILIZATION

(a) with vegetally situated skeleton forming cells *s*, later forming an triradiate spicule. (b) with a secondary ciliary tuft in the same position (from Lindahl, 1936).

unfertilized egg is hardly inhibited at all, whereas an inhibition will appear as soon as the spontaneous rise of respiration, first described by Warburg, takes place. (This phenomenon is considered by Tyler, Ricci and Horowitz (1938) to be the consequence of bacterial activity. However, their experiments show that certain processes in the egg, connected with "ageing", are of importance.) An increased respiration during the treatment thus seems to be the decisive process in animalization. The same is shown by experiments in which the oxygen consumption is accelerated during the treatment, by addition of the reversible redox compound pyocyanine (Runnström and Thörnblom, 1936). The animalizing process is here considerably accelerated. The specific reaction leading to animalization during the treatment thus consists in an oxidation or is coupled

part of the egg will, however, be that least exposed to the inhibitory action emanating from the most animal parts and tending to suppress the animal principle in lower intensity. Thus, this is the only position where a secondary animal pole and apical tuft may arise.

On the localization of certain metabolic processes

The spatial arrangement of the animal and vegetal principles can be demonstrated by micro-surgical methods, but because of the small size of the sea urchin egg—diameter about 80μ —the demonstration of localization of metabolic processes meets with difficulties. Vital staining with redox indicators and the following of reduction under anaerobic conditions have demonstrated the existence of regions with different powers of

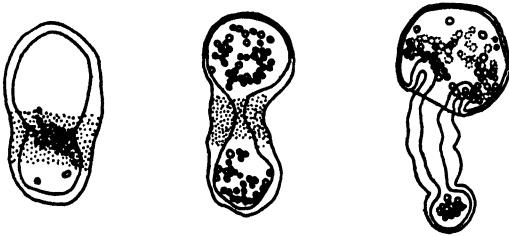


FIG. 7. EMBRYOS OF *PARACENTROTUS LIVIDUS* IN DIFFERENT STAGES OF DEVELOPMENT, ANIMALIZED BY TREATMENT BEFORE FERTILIZATION AND TREATED WITH LITHIUM IONS AFTER FERTILIZATION

The dotting shows the pigment ring of this species lying below the equator in the uncleaved egg (from Lindahl, 1936).

reduction. In oocytes and in various developmental stages up to the late blastula, a reduction gradient exists with the most rapidly reducing region at the animal pole (Child, 1936). Shortly before the migration of skeletal-forming cells a second reduction gradient appears, the primary mesenchyme cells becoming the most rapidly reducing cells of the organism. These two reduction gradients remain until the prism stage, when the gradient pattern becomes more complicated in connection with the formation of stomodeum and arms. Striking is the simultaneous appearance of the vegetal reduction gradient, the sudden commencement of the further increase of respiration and the appearance of toxic intermediary products, normally depoisoned by SO_4^{2-} . Under the action of Li^+ these two reduction gradients are, it is proposed, totally or partly obliterated or even reversed.

The extent of the animal reduction gradient in the blastula stage is said to be closely related to the size of the future ectoderm and to vary, parallel with this, under experimental conditions (Ranzi and Falkenheim, 1937). A limiting value, separating future entoderm and ectoderm, is claimed to have been demonstrated by aid of different rH indicators.

Only the well-known micro methods of Linderström-Lang and Holter have made quantitative measurements in different parts of sea urchin embryos possible. Measurements with aid of the diver method of Linderström-Lang on isolated animal and vegetal halves have shown the respiration to be equal in the two fragments in the 7–9 hour period as well as 12 and 28 hours after fertilization (Lindahl and Holter, 1940). This means that Child's conception of a respiration gradient, with its highest intensity at the animal pole as the basis of polarity, cannot be valid. Because of technical difficulties measurements of respiration on animal and vegetal halves are not possible shortly after fertilization. Though equal in the 7–9 hours stage, the respiration of the two fragments might be different shortly after fertilization, the increasing part of respiration being chiefly limited to the animal half. Against such a localization may be put the equal inhibition or activation of respiration caused by Li^+ , glyceric aldehyde, or pyocyanine in the two halves. (The experiments with Li^+ are here less conclusive, the measurements being performed after the end of the exponential increase of respiration. In this stage the late unspecific kind of inhibition enters.) Although the vegetal reduction gradient appears simultaneously with the sudden commencement of the further increase in respiration shortly before the migration of the primary mesenchyme, this increase seems not to be limited to the vegetal half, the two halves showing the same O_2 -consumption 12 as well as 14 hours after fertilization (Lindahl and Holter, 1940). Thus several facts suggest that the reducing, substrate activating systems of the embryo are not the limiting factors in oxygen consumption, which is more likely to be located in the electron transporting chain of respiration. Similar conditions also seem to be found in the amphibian embryo, where the stated differences in oxygen consumption between different regions of the embryo do not nearly attain the magnitude of those found in anaerobic glycolysis.

Animal and vegetal materials have furthermore been shown to contain equal amounts of dipepti-

dase in early cleavage stages as well as in blastulae and plutei (Holter and Lindahl, 1940) and no changes could be demonstrated during development.

It is thus obvious that a localization of metabolic processes as the basis of the animal and the vegetal principles has not yet been demonstrated.

ON THE DETERMINATION OF THE DORSO- VENTRAL AXIS

If a segmenting sea urchin egg is dissected by meridional cuts, then the fragments obtained, even if they are eighths of the entire egg, acquire dorso-ventral organization. This shows that the determination of the dorso-ventral axis is very labile in this stage and that each part of the circumference may develop into the ventral or dorsal side. What is the mechanism guaranteeing the occurrence of only one ventral side in the normal embryo? Concerning this problem the results of some experiments give information. If unfertilized sea urchin eggs are forced through a narrow pipette and immediately fertilized they maintain elongated form. If this form remains sufficiently during development, two ventral sides (oral fields) appear, one at each of the two ends (Lindahl, 1932). From this result it appears, that a ventral side suppresses the genesis of other ventral sides in the embryo. This conclusion is also supported by constriction experiments (Hörstadius, 1938). If the distance between two parts of the circuit of the egg equator exceeds a certain value, or if the contact between such parts is greatly diminished by a constriction, the suppressive action of the ventral side does not assert itself through the entire egg.

Certain facts indicate that the ventral side arises independently of the point of entrance of the sperm (Hörstadius, 1928) but is conditioned by certain local colloidal structures of the cortex (Förster and Örström, 1933). It seems further to be favored in some respects in reference to other parts of the egg and is thus superior to them, as may be concluded from experiments with stretched eggs (Lindahl, 1932). Here the end of the egg, which passes first through the narrow pipette and which is subjected to a stretching, develops into the ventral side. If, however, this end is poisoned by very strong vital staining with Nile Blue Sulfate, then the other end, which is now relatively favored, becomes the ventral side. This view is further supported by recent experiments by Pease (1940), in which the eggs are brought during

cleavage into a diffusion gradient of various poisons, the part of the egg treated with the lowest concentration developing into the ventral side. Moreover, we know that stretching of eggs by means of centrifuging increases the activity of the indophenol blue oxidase (Navez and Harvey, 1935) as well as of the normal dehydrogenase system (Ballentine, 1940). Unpublished experiments of H. Holter and the author have, however, shown the respiration to be equal after fertilization in normal eggs and in those stretched by means of a narrow pipette.

It is possible to influence the position of the ventral side and consequently also the dorso-ventral axis by centrifuging (Runnström, 1925; Lindahl, 1932; Pease, 1939). The protoplasmic inclusions accumulated in one part of the egg and remaining there during development, seem to be the important factor, the ventral side arising in that part or its neighborhood. One cannot escape from the impression, that the presumptive "pre-existing" dorso-ventral polarity, in many cases of centrifuged eggs, co-operates with the stratified inclusions in localizing the ventral side, since it often appears at some distance from the former (Lindahl, 1932). This fact led Pease (1939) to the hypothesis, that the ventral side in the normal egg is determined by at least two factors, one of which is a cortical gradient and the other a diffusely distributed substance in the interior. In the centrifuged egg the ventral side is thought to be determined in the region of the greatest interactivity between these two systems.

Measurements on eggs fragmented by centrifugation show a higher dehydrogenase activity of centrifugal fragments than of centripetal ones, which suggests that part of the dehydrogenase system is associated with the granular material (Ballentine, 1940). Centrifugal fragments show a higher respiration than centripetal ones (Shapiro, 1935). At fertilization the oxygen consumption of the latter rises, and becomes about the same in the two types of fragments.

There thus appear certain possibilities of associating the experimentally induced local "favoring," which leads to the development of the ventral side at a certain place, with local changes in metabolism. Especially interesting are the experiments of Pease already mentioned. Here the eggs are brought into a concentration of various substances, of which cyanide, picric acid, 2,4 dinitrophenol, urethane, iodoacetic acid, iodine

and ferricyanide were effective in orienting the dorso-ventral axis, the most inhibited region becoming dorsal, the least inhibited ventral. Experiments performed with malonic acid, arsenate, heavy metal salts, and various alkaloids gave negative results. The fact that local inhibition of cleavage does not necessarily modify the bilateral determination leads to the conclusion that this is not dependent upon a vague "metabolic gradient," but upon a specific enzyme (Pease, 1940). As the whole respiration of the sea urchin egg according to recent results (Lindahl, 1939) must be considered to be cyanide sensitive, the experiments with KCN show that oxidation-reductions are involved under these conditions.

A further very much discussed result may be explained by the fact that the ventral side suppresses the genesis of other ventral sides. When 2—32 cell stages are cut frontally the dorso-ventral axis of the dorsal fragment is inverted. The ventral side thus takes the place of the original dorsal side. It further differentiates much more slowly than the ventral side of the ventral fragment. In the entire embryo, the original dorsal side is the region that has been the least exposed to the suppressive action of the ventral side and is thus the favored region in the dorsal fragment.

Many facts show a close relation to exist between the origination of the dorso-ventral axis and the animal and vegetal principles. Thus the size of the ventral differentiations of the ectoderm, the ciliated band and the oral field are conditioned by the animal-vegetal relation. In animalized embryos they increase at the cost of the low dorsal epithelium, in vegetalized embryos they decrease. From certain stretching experiments the author (Lindahl, 1932, 1936) concluded, that a co-operation of animal and vegetal qualities is necessary for the origination of the organizing presumptive ventral side. The isolation experiments of Hörstadius supplement this view very well. The most extreme animal and vegetal fragments develop into radially symmetrical structures. If, however, they are united in one embryo, bilateral organization appears.

Several attempts have been made to relate hypothetically the origination of the dorso-ventral organization with the animal and vegetal principles. On the one side an oblique course of the vegetal gradient has been purposed (Runnström,

1928; Schleip, 1929), the ventral side being more vegetal than the dorsal one. On the other hand the possibility is discussed that *both* the principles are realized to a higher degree on the ventral than on the dorsal side (Lindahl, 1932, 1936). The latter state could possibly be attained by more favorable diffusion conditions for specifically acting substances provided by special colloid structures on the ventral side. As a matter of fact the protoplasmic colloids of the ventral side behave differently from those of the dorsal side. In favor of these two hypotheses observations on vegetalized, constricted and stretched embryos are quoted. A decision by means of microrurgical experiments seems possible only for the first hypothesis. The experiments performed hitherto do not show any greater extension of the vegetal qualities on the ventral than on the dorsal side (Hörstadius and Wolsky, 1936).

The indispensability of co-operation between the two principles for the origination of the dorso-ventral organization has been established. On the other hand it is debatable whether the existence of vegetal and animal qualities in higher intensity on the ventral than on the dorsal side is to be looked at rather as a consequence than as a condition. Certain cases in which great local discontinuities in the "morphogenetic gradients" are experimentally applied, without determining the ventral side (Hörstadius, 1939), suggest that such conditions cannot in themselves be deciding. At present the assumption of a "favored" region, in elongated eggs the stretched end, in fragments and fused embryo parts the presumptive ventral side, seems to offer sufficient explanation.

The determination of the asymmetry axis is governed by conditions similar to that of the dorso-ventral one. Here also we are dealing with a heteropolar axis, the left-right one which becomes the apico-basal axis of the adult sea urchin. At both ends of this axis hydrocoeles may be formed. The obvious favoring of the one side, in normal development the left one, suppresses the formation of a hydrocoel on the other side (Hörstadius, 1933), thus determining the polarity of the axis. However, there is a great difference. The dorso-ventral axis may fall in each meridional plane, whereas the *direction* of the asymmetry axis is already determined by the fixation of the dorso-ventral axis.

LIST OF LITERATURE

- BALLENTINE, R. 1940. Quantitative cytochemistry. The distribution of the reducing systems in the egg of *Arbacia punctulata*. *Jour. Cell. and Comp. Physiol.*, 16: 39-47.
- CHILD, C. M. 1916. Experimental control and modification of larval development in the sea-urchin in relation to the axial gradients. *Jour. Morph.*, 28: 65-133.
- . 1916. Axial susceptibility gradients in the early development of the sea-urchin. *Biol. Bull.*, 30: 391-405.
- . 1936. Differential reduction of vital dyes in the early development of Echinoderms. *Arch. f. Entomech.*, 135: 426-456.
- . 1940. Lithium and Echinoderm exogastrulation: With a review of the physiological gradient. *Physiol. Zool.*, 13: 4-42.
- EPHRUSSI, B., and L. RAPKINE. 1928. Composition chimique de l'oeuf d'oursin *Paracentrotus lividus* Lk. et ses variations au cours du développement. *Ann. Physiol. et Physicochem. Biol.*, 4: 386-398.
- FÖRSTER, M., and A. ÖRSTRÖM. 1933. Observations sur la predetermination de la partie ventrale dans l'oeuf d'oursin. *Trav. Sta. Biol. Roscoff*, 11: 63-.
- GRAY, J. 1927. The mechanism of cell division. III. The relationship between cell-division and growth in segmenting eggs. *Brit. Jour. Exper. Biol.*, 4: 313-321.
- HAYES, F. R. 1938. The relation of fat changes to the general chemical embryology of the sea-urchin. *Biol. Bull.*, 74: 267-277.
- HOLTER, H., and P. E. LINDAHL. 1940. Beiträge zur enzymatischen histochemie. XXXII. Über die verteilung der peptidase in Paratrotus-keimen. *C. R. Trav. Labor. Carlsberg, Ser. Chim.*, 23: 249-256.
- HÖRSTADIUS, S. 1928. Über die Determination des Keimes bei Echinodermen. *Acta Zool.*, 9: 1-191.
- . 1935. Über die Determination im Verlaufe der Eiachse bei Seeigeln. *Pubbl. Staz. Zool. Napoli*, 14: 251-429.
- . 1936. Über zeitliche Determination im Keim von *Paracentrotus lividus* Lk. *Arch. f. Entomech.*, 135: 1-39.
- . 1938. Schnurtingsversuche an Seeigelkeimen. *Arch. f. Entomech.*, 138: 197-258.
- . 1939. The mechanics of sea-urchin development, studied by operative methods. *Biol. Rev. Cambridge Philosoph. Soc.*, 14: 132-179.
- HÖRSTADIUS, S., and S. STRÖMBERG. 1940. Untersuchungen über Umdeterminierung von Fragmenten des Seeigeleies durch chemische Agentien. *Arch. f. Entomech.*, 140: 409-462.
- , and A. WOLSKY. 1936. Studien über die Determination der bilateral Symmetrie des jungen Seeigelkeimes. *Arch. f. Entomech.*, 135: 69-113.
- KUHN, R., and K. WALLENFELS. 1939. Über die chemische Natur des Stoffes den die Eier des Seeigels (*Arbacia pustulosa*) absondern, um die Spermatozoen anzulocken. *Ber. d. Deutsch. Chem. Ges.*, 722: 1407-1413.
- LEHMANN, H., and J. NEEDHAM. 1938. The action of glycerinaldehyd on carbohydrate breakdown. *Enzymologia*, 5: 95-.
- LINDAHL, P. E. 1932a. Zur experimentellen Analyse der Determination der Dorsoventralachse beim Seeigelkeim. I. Versuche mit gestrickten Eiern. *Arch. f. Entomech.*, 127: 300-322.
- . 1932b. II. Versuche mit zentrifugierten Eiern. *Arch. f. Entomech.*, 127: 323-338.
- . 1933. Über 'animalisierte' und 'vegetativisierte' Seeigellarven. *Arch. f. Entomech.*, 128: 661-664.
- . 1935. Über die Rolle des SO_4 -ions in der Entwicklung des Seeigelkeims. *Ark. f. Zool.*, 28 B: No. 4, 1-4.
- . 1936. Zur Kenntnis der physiologischen Grundlagen der Determination im Seeigelkeim. *Acta Zool.*, 17: 179-365.
- . 1939. Zur Kenntnis der Entwicklungsphysiologie des Seeigeleies. *Ztschr. f. vergl. Physiol.*, 27: 233-250.
- . 1940. Neue Beiträge zur physiologischen Grundlage der Vegetativisierung des Seeigelkeimes durch Lithiumionen. *Arch. f. Entomech.*, 140: 168-194.
- , and H. HOLTER. 1940. Die Atmung animaler und vegetativer Keimhäften von *Paracentrotus lividus*. *C. R. Trav. Labor. Carlsberg, Ser. chim.*, 23: 257-288.
- , and L. O. ÖHMAN. Weitere Studien über Stoffwechsel und Determination im Seeigelkeim. *Biol. Zentralbl.*, 58: 179-218.
- , and A. STORDAL. 1937. Zur Kenntnis des vegetativen Stoffwechsels im Seeigeli. *Arch. f. Entomech.*, 136: 44-63.
- NAVEZ, H. E., and E. B. HARVEY. 1935. Indophenol oxidase activity in intact and fragmented *Arbacia* eggs. *Biol. Bull.*, 69: 342 (Abstract).
- NEEDHAM, J. 1939. Developmental physiology. *Ann. Rev. Physiol.*, 1: 63-80.
- NEEDHAM, J., and D. M. NEEDHAM. 1940. A note on the biochemistry of embryonic determination in Echinoderms. *Jour. Exper. Biol.*, 17: 147-152.
- ÖHMAN, L. O. 1940. Über die Veränderung des respiratorischen Quotienten während der Frühentwicklung des Seeigeleies. *Ark. f. Zool.*, 32 A: no. 15, 1-9.
- PEASE, D. C. 1939. An analysis of the factors of bilateral determination in centrifuged Echinoderm embryos. *Jour. Exper. Zool.*, 80: 225-247.
- . 1940. Echinoderm bilateral determination in

- chemical concentration gradients. I. The effects of cyanide, ferricyanide, picrate, etc. *Jour. Exper. Zool.*, 86: 381-404.
- RANZI, S. 1939. Ricerche sulle basi fisiologiche della determinazione negli embrioni degli Echinodermi. II. Influenza del solfocianuro. *Arch. zool. Ital.*, 26: 427-440.
- , and M. FALKENHEIM. 1937. Ricerche sulle basi fisiologiche della determinazione nell'embrione degli Echinodermi. *Pubbl. Staz. Zool. Napoli.*, 16: 436-458.
- RUNNSTRÖM, J. 1925a. Experimentelle Bestimmung der Dorso-ventral-achse bei dem Seeigelkeim. *Ark. f. Zool.*, 18 A: no. 4, 1-6.
- . 1925b. Über den Einfluss des Kaliummangels auf das Seeigelei. *Pubbl. Staz. Zool. Napoli.*, 6: 1-200.
- . 1928a. Zur experimentellen Analyse der Wirkung des Lithiums auf den Seeigelkeim. *Acta Zool.*, 9: 365-424.
- . 1928b. Plasmabau und Determination bei dem Ei von *Paracentrotus lividus* Lk. *Arch. f. Entomech.*, 113: 556-581.
- . 1929. Über Selbstdifferenzierung und Induktion bei dem Seeigelkeim. *Arch. f. Entomech.*, 117: 123-145.
- . 1931. Zur Entwicklungsmechanik des Skelettmusters bei dem Seeigelkeim. *Arch. f. Entomech.*, 124: 273-297.
- . 1935. An analysis of the action of lithium on sea-urchin development. *Biol. Bull.*, 68: 378-384.
- , and D. THÖRNBLÖM. 1936. Über den Einfluss von Pyocyanin auf die durch ca-freies Seewasser-natriumrhodanid bewirkte animalisierung des Seeigeleies. *Naturwiss.* 24: 447- (Abstract).
- SCHACTER, V. 1937. Calcium reduction and the prolongation of life in the egg cells of *Arbacia punctulata*. *Biol. Bull.*, 72: 366-376.
- SCHLEIP, W. 1929. Die Determination der Primitiventwicklung. *Leipzig*.
- UBISCH, L. v. 1925. Entwicklungsphysiologische Studien an Seeigelkeimen. III. Die normale und durch Lithium beeinflusste Anlage der Primitivorgane bei animalen und vegetativen Halbkeimen von *Echinocyamus pusillus*. *Ztschr. f. Wiss. Zool.*, 124: 469-486.
- . 1936. Über die Organisation des Seeigelkeims. *Arch. f. Entomech.*, 134: 599-652.
- WARBURG, O. 1915. Notizen zur Entwicklungsphysiologie des Seeigeleies. *Arch. f. ges. Physiol.*, 160: 324-332.





RUDIMENTARY DIGITS IN PRIMATES

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THE Primates are among the most generalized of mammals in that they possess five well-developed digits on both manus and pes. While this is true of most members of the order, a few forms nevertheless depart from the ordinal rule. In these species, one or more digits normally are so under-developed that they must be regarded as stunted or even rudimentary. This condition usually is more than merely dimensional in nature, for, as will be shown, it commonly involves external characters, skeleton, and musculature. Such type of stunted digit, normal for a given species, falls into a different category from those anomalous rudiments that occasionally occur in man and other primates as well (see Schultz, 1942). The latter do not lie within the scope of this paper.

FOOT

Fifth toe

Man. As is well known, the fifth toe of man decidedly is disposed toward a stunted condition. Wood Jones (1918, p. 79) has succinctly described its dwarfed nature:

Usually it is but a poor thing; its nail is ill developed, and at times no nail is present. It is peculiarly liable to that circulatory disturbance which manifests itself in chilblains, and not uncommonly it seems in a poor state of nutrition. Most people possess but little power of movement in it, and its skeleton shows that its atrophic condition has affected the bones and joints, for the last two phalanges are very commonly fused together, making it short of a joint as compared with the rest of the toes. Very commonly its axis is not straight, and the toe is humped up and also somewhat bent laterally.

He also pointed out that this cannot be attributed to the wearing of shoes, as often believed, since the little toe exhibits similar characteristics in bare-footed groups of man.

Fusion of the last two phalanges of the fifth toe,

or lack of the middle phalanx—sometimes called “brachyphalangy”—is not uncommon in both whites and Negroes (cf. Pfitzner, 1896; Schultz, 1926a; Straus, 1927) and is normal in Japanese (Adachi, 1905; Hasebe, 1912). Its occurrence in fetuses proves its congenital nature (Schultz, 1926a; Straus, 1927).

The muscles of the fifth toe, however, are not uniquely atrophic in man. On the plantar surface, as normally in other primates, there is a long flexor tendon, a tendon from the flexor digitorum brevis, an abductor digiti quinti, a lumbrical, a flexor-opponens digiti quinti brevis, and a plantar interosseous. The tendon of the flexor digitorum brevis, however, is absent in some 20 per cent or more of individuals; yet the anthropoid apes also are in default of this tendon at least as frequently (Straus, 1930a). The lumbrical muscle likewise may be lacking, but possibly no more often than that of other toes. A contrahens digiti quinti, a basic pedal muscle, does not occur in man; but its normal suppression again is shared with the three great anthropoid apes.

Dorsally, man's fifth toe possesses a digital tendon from the extensor digitorum longus, while a peroneus brevis and a peroneus tertius are inserted upon its metatarsal bone. The latter, as a normal structure, is indeed a human peculiarity, although appearing as a variant in other catarrhine primates, notably the gorilla (cf. Straus, 1930a; Wells, 1935). A second extensor of the minimus, the peroneus digiti quinti, is normal for lemurs, *Tarsius* and monkeys; it is lacking, except as a rudimentary variant, not only in man but in the anthropoid apes as well (Straus, 1930a).

The muscles of the fifth toe, therefore, do show certain atrophic tendencies in both man and the anthropoid apes when comparison is made with other primates. But the skeleton of this digit seems to be affected only in man; for, to my knowledge, brachyphalangy or a similar condition has not been reported for any other primate.

Second toe

Among primates as a whole, the second toe is well-developed. There are three phalanges, of which the terminal bears a nail. On them are inserted eight muscles: 6 plantar—a long flexor tendon (from the flexor digitorum tibialis or the flexor digitorum fibularis, or both), a short flexor tendon (from the flexor digitorum brevis), a lumbrical, a contrahens, and a pair of interossei—and 2 dorsal—a tendon from the extensor digitorum longus and a slip of the extensor digitorum brevis.

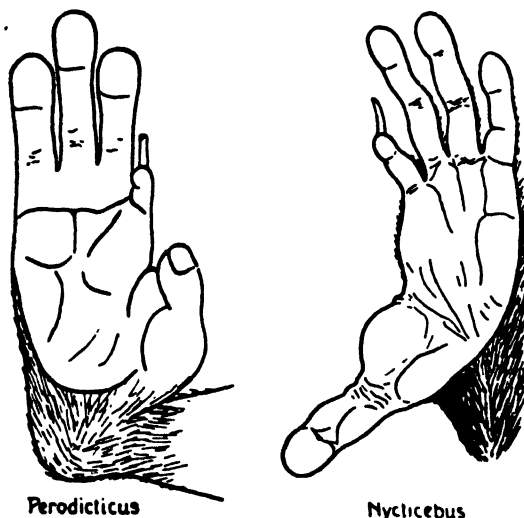


FIG. 1. RIGHT FOOT OF THE POTTO, *PERODICTICUS* (AFTER MIDLO), AND LEFT FOOT OF THE SLOW LORIS, *NYCTICEBUS* (FROM MIDLO, AFTER MURIE AND MIVART)

The pincers-like form of the foot in *Nycticebus* clearly is evident; this is concealed in the drawing of *Perodicticus*, for the hallux is shown in a somewhat adducted position.

Lorisidae. The slow lemurs, forming the family Lorisidae, all possess stunted second toes. In the lorises, *Nycticebus* (Fig. 1) and *Loris*—so closely related zoologically that they often are confused with each other—the second pedal digit is relatively quite short. Although there are three phalanges, these are comparatively abbreviated, the middle being especially small. A nail, claw-like as in other lemurs, is present. The foot musculature has been rather thoroughly described by Murie and Mivart (1872), while Ruge (1878, a and b), Glaesmer (1910), Sawalischin (1911) and Forster (1933b) have supplied additional information. The muscular equipment

of the second toe appears to be complete save for the frequent absence of a tendon from the flexor digitorum brevis (absent in 4 *Nycticebus*: Murie and Mivart (1), Forster (3); present in 4 *Nycticebus*: Sawalischin; present in 1 *Loris*: Glaesmer) and the lack of the lumbrical (in *Nycticebus*: Murie and Mivart). The former condition is virtually unique among primates, but this particular lumbrical occasionally is missing in catarrhine monkeys (Ribbing, 1909) and man (Le Double, 1897). The tendon of the extensor digitorum longus is weaker than the corresponding slips to the other toes, this in both genera (Murie and Mivart); yet this also can occur in catarrhine primates (Straus, 1930a).

In the other Lorisidae, namely, the potto, *Perodicticus* (Fig. 1), and the closely allied angwán-

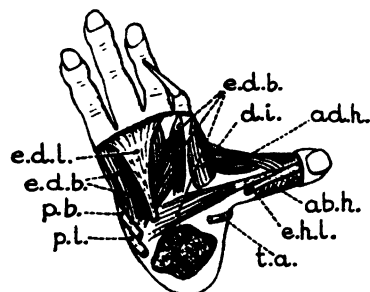


FIG. 2. DORSAL ASPECT OF THE LEFT FOOT OF *PERODICTICUS POTTO*

The pincers-like arrangement resembles that of *Nycticebus*. Note the absence of a tendon from the extensor digitorum longus (e. d. l.) to the stunted second toe.

tibo, *Arctocebus*, the second toe similarly is stunted (for *Arctocebus*, see Huxley, 1864a). The external and skeletal characters resemble those of the *Nycticebus-Loris* group. The associated musculature, however, differs somewhat, at least in *Perodicticus*. A description of the myology of *Arctocebus* seems not to have been published, and no specimen was available to me for study. The following account of the muscles of *Perodicticus* is derived from my dissection of a specimen of *P. potto* (W. L. S.), supplemented by data given by Van Campen (1859), Glaesmer (1910), Hunter (1925), MacKenzie (1931), and Forster (1933b). For the second toe, there is the normal primate complement except for the regular absence of a tendon from the extensor digitorum longus, which is present but weak in the other lorises (Fig. 2). This tendon was wholly lacking in 4 animals (Hunter, MacKenzie, Van Campen, W. L. S.),

present as a thin filament in one other (Forster). It should be noted, however, that absence of said tendon is not entirely peculiar to the pottos, although a normal character in them alone: for it occasionally is missing in orang-utans and colobine

—long flexor, lumbrical, contrahens, interossei, short extensor—to be well-developed.

Hallux

As a rule, the hallux, or vernacular "big toe", is strongly developed in primates. Upon its two phalanges are inserted six muscles, 4 plantar—a long flexor tendon (derived from one or both of the long crural digital flexors), an abductor hallucis, a flexor hallucis brevis, and an adductor hallucis—and 2 dorsal—an extensor hallucis longus and a slip of the extensor digitorum brevis—while to its metatarsal bone are attached the peroneus longus and a portion of the tibialis anterior.

Orang-utan. Of all primates, only the orang-utan possesses a rudimentary hallux (Fig. 3). Indeed, its stunting is far more extreme than that of any digit thus far discussed. Absence of the terminal phalanx occurred in over half the cases studied by Schultz (1941) and always was accompanied by absence of the nail. Yerkes and Yerkes (1929) suggested that this condition may be the result of self-mutilation brought on by dietary deficiency, endocrine disturbance, or some neuropathic state. Its occurrence in fetal life (Schultz,

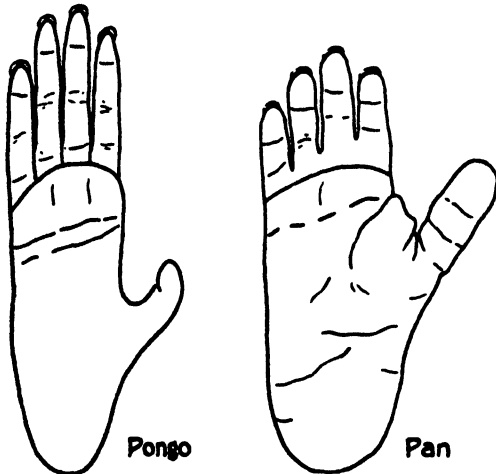


FIG. 3. RIGHT FEET OF ORANG-UTAN (PONGO) AND CHIMPANZEE (PAN). BOTH AFTER MIDLO
The rudimentary hallux of the orang contrasts markedly with the powerful hallux of the chimpanzee.

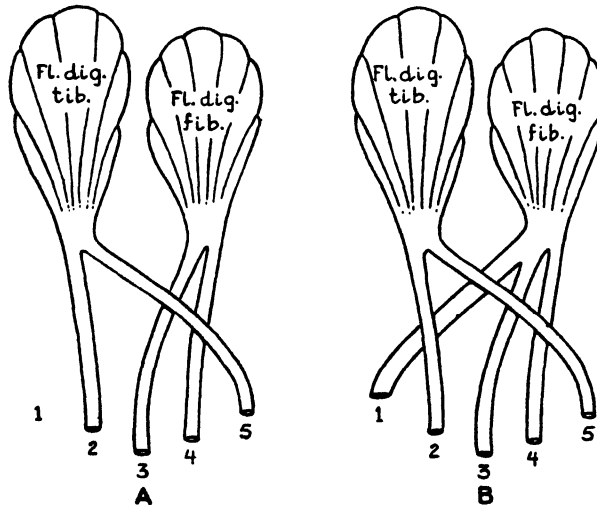


FIG. 4. DIAGRAMS SHOWING THE ARRANGEMENT OF THE LONG FLEXOR MUSCLES OF THE TOES—FLEXOR DIGITORUM TIBIALIS AND FLEXOR DIGITORUM FIBULARIS—IN ORANG-UTAN (A) AND CHIMPANZEE AND GORILLA (B)

The orang normally has no trace of a tendon to the hallux.

monkeys (cf. Straus, 1930a), and even, as an extremely rare anomaly, in man. The tendon of the flexor digitorum brevis to the second toe of *Perodicticus*, furthermore, may be weak (W. L. S.) or even rudimentary (Forster). On the other hand, I found the remaining muscles of that digit

1936), however, is sufficient negation of such traumatic origin.

The foot musculature of an orang that I studied already has been reported upon together with data from the literature (Straus, 1930a). In general, the orang regularly possesses the full complement

of hallucal muscles, save that—in correlation with the abortive character or absence of the terminal phalanx—a long flexor tendon normally is wholly absent (Fig. 4, A). Of 23 orang-utans reported upon (Barnard; Beddard; Bischoff, 1870; Boyer; Brooks, 1888; Chapman, 1880; Church; Fick, 1895a and 1895b (2 animals); Glaesmer; Gratiolet and Alix; Hafferl; Hartmann; Hepburn; Huxley, 1864b; Langer; Michaelis; Owen; Primrose; Sonntag, 1924; C. Stewart; Straus, 1930a; Testut, 1884), this tendon was entirely lacking in 21 animals. Of the remaining two, one possessed a functionless rudiment disconnected from muscle

more marked stunting implicates the corresponding digit of their hands.

In both *Nycticebus* and *Loris*, the index finger possesses three phalanges and a nail. The phalanges—especially the middle and terminal—however, are comparatively quite short, producing a stunted appearance (Fig. 5). Among primates, eight muscles normally are inserted upon the second finger, of which 6 are volar—a tendon from the flexor digitorum sublimis, one from the flexor digitorum profundus, a lumbrical, a contrahens and 2 interossei, sometimes subdivided—and 2 dorsal—a tendon from the extensor digitorum

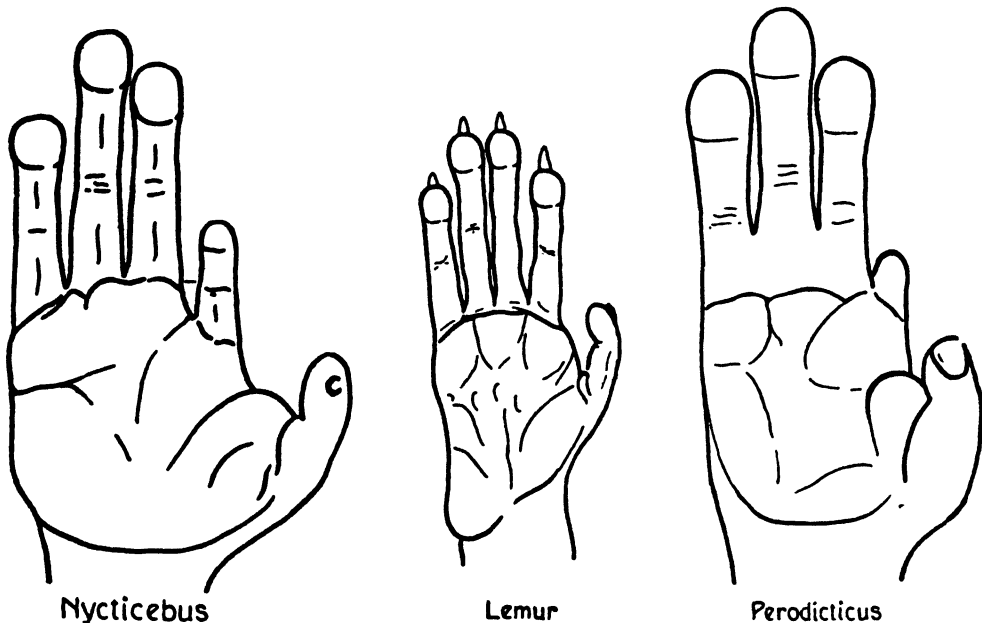


FIG. 5. RIGHT HANDS OF NYCTICEBUS, LEMUR AND PERODICTICUS. ALL AFTER MIDLO

The pincers-like form of the manus in *Nycticebus* and *Perodicticus* is not evident, for their thumbs are pictured somewhat adducted. The second finger is stunted in *Nycticebus* and a mere rudiment in *Perodicticus*, this contrasting strikingly with *Lemur*.

fibers and restricted to the hallux itself (Bischoff); the other had a hallucal tendon from the flexor digitorum tibialis (Barnard). The presumed rudiments described by Brooks and Langer fall into the doubtful category.

These hallucal characters of the orang-utan are unique among the primates and are not even suggested in any other member of the order.

HAND

Second finger

Lorisidae. The *Lorisidae*, as noted above, differ from other lemurs in their tendency toward dwarfing of the second toe. A similar but even

communis, and one from the extensor digitorum profundus. The flexor carpi radialis and the extensor carpi radialis longus are attached to the base of the metacarpal bone. Data for the muscles of *Nycticebus* and *Loris* are given by Murie and Mivart (1872), Kajava (1911), and Forster (1917). In these animals, the musculature of the index finger apparently is normal except for the absence of the tendon from the flexor digitorum sublimis. Defaunt of this particular tendon has not been reported, in my knowledge, for any primate save the *Lorisidae*, except as an extremely rare anomaly in man (cf. Le Double).

The index finger of both *Perodicticus* and *Arc-*

tocebus is far more stunted, being truly rudimentary. Externally, that digit appears as little more than a nailless tubercle (Fig. 5). In *Perodicticus*, there are but two short phalanges, and even the metacarpal bone is abbreviated. *Arctocebus* is identical in this respect (Huxley, 1864a; Elliot, 1913). The associated musculature of *Perodicticus* is extremely deficient (Fig. 6, A). There is no long flexor tendon from either the flexor digitorum sublimis or the flexor digitorum profundus (Forster, 1933b; Van Campen; W. L. S.), no lumbrical (Kajava, 1911; W. L. S.), and no tendon from the extensor digitorum communis (Forster, 1933, a and b; Van Campen; Straus, 1941). A distal

the two phalanges and metacarpal bone of the primate thumb, 5 volar—a tendon of the flexor digitorum profundus (or its flexor pollicis longus portion), an abductor pollicis brevis, a flexor pollicis brevis superficialis, an opponens pollicis, and an adductor pollicis—and 2 dorsal—an extensor pollicis longus, either separate or as a slip of an extensor pollicis et indicis longus, and an abductor pollicis longus. A flexor pollicis brevis profundus (interosseus volaris primus of Henle) is of very irregular and variable occurrence throughout the entire order. The extensor pollicis brevis, of late evolutionary appearance, is constant only in man (Straus, 1941).

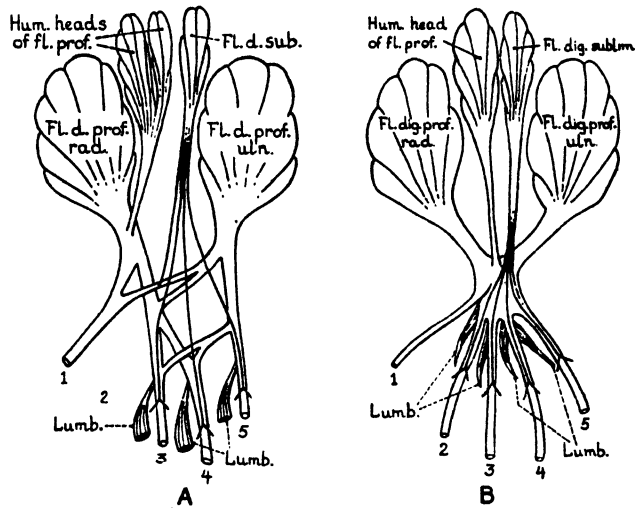


FIG. 6. DIAGRAMS OF THE LONG FLEXOR MUSCLES OF THE FINGERS AND THE ASSOCIATED LUMBRICAL MUSCLES IN *PERODICTICUS* (A) AND *LEMUR* (B)

Lemur, which possesses an essentially generalized primate arrangement of these muscles, is included for comparison with *Perodicticus*. Note that there are no long flexor tendons (from flexor digitorum sublimis and flexor digitorum profundus) and no lumbrical for the second finger of *Perodicticus*.

rudiment of the last-named possibly may occur, however (Straus, 1941). The other normal primate muscles are present. No data for *Arctocebus* are obtainable.

Thumb

The thumb is more liable to defective or incomplete development than any other primate digit. This phenomenon, moreover, has a relatively wide familial distribution, occurring in both platyrrhine—*Ateles*, *Brachyteles*—and catarrhine Anthropoidea—*Colobus*, orang-utan, chimpanzee, gorilla. It affects neither Lemuroidea nor Tarsiioidea, however.

There regularly are seven muscles attached to

Atelinae. The coaitas or spider monkeys *Ateles* and *Brachyteles*, of the platyrrhine family Cebidae, normally lack an external thumb (Figs. 7 and 9, no. 7), hence their generic names (*ateles*, Gr., meaning "without end" or "imperfect"). Their variability respecting this feature has been thoroughly discussed by both Pocock (1925) and Schultz (1925, 1926b). An external thumb can appear in both genera (Fig. 9, no. 6), but is relatively rare in *Ateles* at least. In this genus, Schultz (1926b) found a free thumb in only 2 (in both unilaterally) of 58 animals.

Even though there be no external pollex, its rudimentary skeleton regularly is present, hidden beneath the skin. This usually comprises a small

metacarpal bone and a single, minute phalanx (Elze, Flower, Leche, Huxley, 1883). Elze (1910) believed that the phalanx actually represented a sesamoid bone, but there seems to be no doubt of its true phalangeal nature in some specimens.

When an actual external thumb occurs, this contains a metacarpal bone accompanied by either two fused phalanges (Schultz) or a single prominent phalanx (W. L. S.). In an adult *Ateles geoffroyi* (J. H. Anat. no. 351) that I dissected, a well-developed though short external thumb appeared on each hand. On the right hand, this measured 13.5 mm. from free base to tip and had a mean circumference of about 23 mm. There was no trace of a nail. Internally, there was a rather stout metacarpal bone 25 mm. long (metacarpale II was 45 mm. long) and a single phalanx 16 mm. long and 2.5 mm. wide and 2 mm. thick at its middle.

The pollical musculature of *Ateles* generally is rudimentary, although variable in its development. The following discussion is based upon three specimens of *Ateles geoffroyi* that I studied (J. H. Anat. nos. 47, 150, and 351, all collected by Dr. A. H. Schultz in Chiriqui), as well as upon the literature. My notes for no. 150 unfortunately are incomplete. No. 351 possessed an external thumb (*vide supra*), while nos. 47 and 150 both had only the customary internal rudiments. In normal coaitas, lacking outer thumbs there is no trace of a long pollical flexor tendon (Boas; Elze; Huxley, 1864b; Meckel, cit. by Kohlbrügge, 1897, and Gruber; Senft; Wilder; W. L. S.: nos. 47 and 150) (Fig. 11, C); but in no. 351, with an external pollex, there was an undoubted though functionless distal rudiment—a thin tendinous cord that arose diffusely from the areolar tissue deep to the flexor digitorum profundus over the mid-carpal region and pursued the customary primate course along the volar surface of the thumb, to disappear in the subcutaneous connective tissue over the distal end of the phalanx (Fig. 11, B). Similarly, there normally is no long extensor tendon for the thumb (Senft, C. Stewart, W. L. S.: no. 47); yet in no. 351, the pollical phalanx received a slip from the slender tendon of an extensor pollicis et indicis longus, a muscle habitual to other platyrrhines (see Straus, 1941). A strong abductor pollicis longus always occurs (Senft, C. Stewart, Wilder, W. L. S.: nos. 47, 150, 351).

The short muscles of the thumb at times are very clearly differentiated. In no. 351, I found

(1) a definite abductor pollicis brevis arising from the radial sesamoid bone of the carpus; (2) a well-developed flexor pollicis brevis superficialis, from the transverse carpal ligament; (3) a strong opponens pollicis with like ligamentous origin; (4) a thin adductor pollicis arising from the base of metacarpale III and from a raphe extending forward to the head of that bone; and (5) a slender flexor pollicis brevis profundus with origin from the ulnar border of metacarpale I. The opponens was inserted as in other primates upon the radial border of the first metacarpal bone. The four other muscles had their customary primate inser-

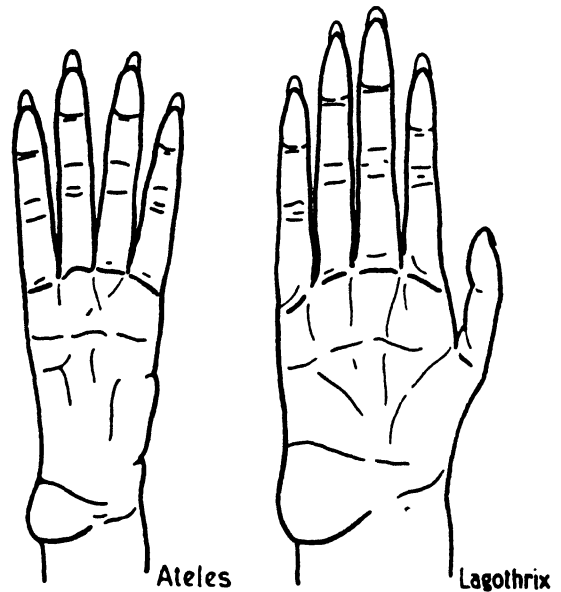


FIG. 7. RIGHT HANDS OF THE COAITA, ATELES, AND THE CLOSELY RELATED WOOLLY MONKEY, LAGOTHRIX. BOTH AFTER MIDLO

Ateles normally lacks an external thumb, whereas that digit is well-developed in *Lagothrix*.

tions upon the pollical phalanx, and not at all upon the metacarpal bone.

In my two other specimens, lacking outer thumbs, the muscles were far less differentiated. Animal no. 150 exhibited a rather well-developed adductor pollicis that was inserted on the head of metacarpale I; beyond this, there were other fibers, inserted similarly, representing the remaining, undifferentiated thenar musculature. Even more rudimentary conditions obtained in no. 47, for the thenar complex appeared as one small fan-shaped mass inseparable into nameable components.

Other specimens of *Ateles*, described in the

literature, exhibited similar variability. Huxley (1864b) apparently found all of the four usual primate thenar muscles—abductor, flexor, opponens, adductor—while Leche noted all except the abductor. Only two muscles were found in the specimens of Senft (flexor and adductor) and Forster (1917, abductor and adductor). Finally, Wilder discovered only rudiments. The insertions in these animals (save possibly that of Senft) seem to have been only upon the distal part of the metacarpal bone, and not upon the phalanx.

The muscles of *Brachyteles* appear not to have been studied.

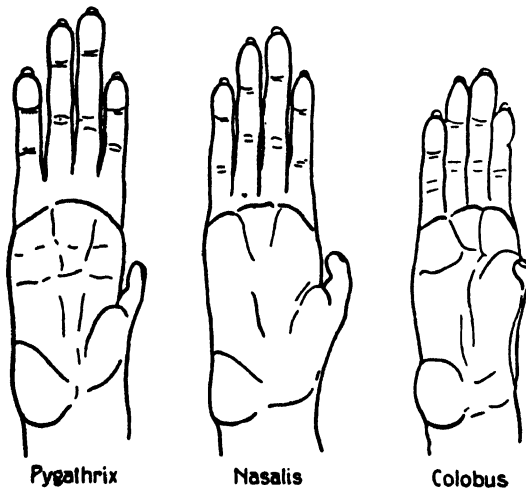
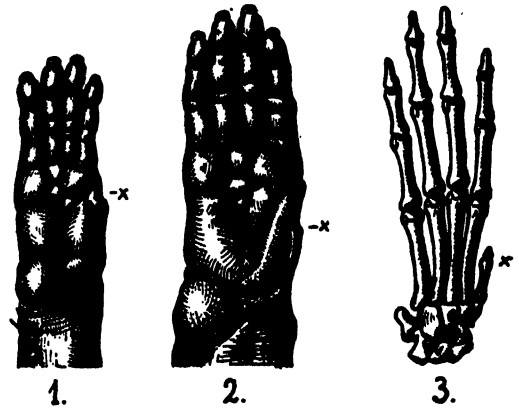


FIG. 8. RIGHT HANDS OF LANGUR (*Pygathrix*), PROSCIS MONKEY (*Nasalis*) AND GUEREZA, FETUS (*Colobus*). ALL AFTER MIDLO

The thumb is short in *Pygathrix* and *Nasalis*, rudimentary in *Colobus*.

Colobus. The guereza, *Colobus*, of the catarrhine sub-family Colobinae (*sive* Semnopithecinae), approximates the platyrrhine Atelinae in the normal possession of a rudimentary thumb (cf. Pocock, 1926; Schultz, 1924, 1926b), thus its generic name (*kolobos*, Gr., meaning "curtailed", or "incomplete", or "mutilated") (Figs. 8 and 9, nos. 1-3). Schultz has shown that while an outer

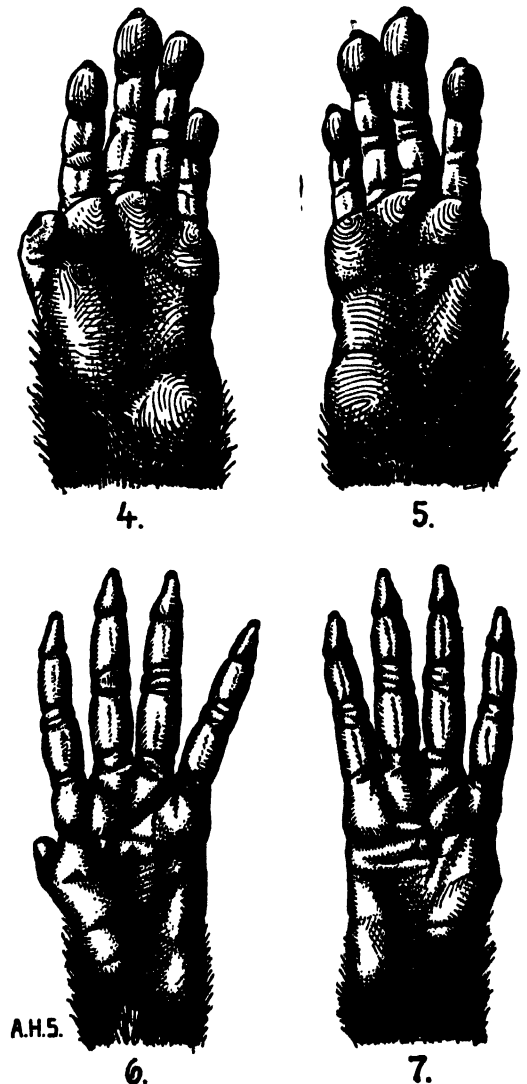


FIG. 9. DEFICIENCY OF THE THUMB IN MONKEYS

Nos. 1-3, right hands of the guereza, *Colobus*, showing rudimentary thumbs at X (1, fetus, 112 mm. sitting height; 2, fetus, 134 mm. sitting height; 3, adult lacking external thumb, skeleton only). Nos. 4 and 5, hands of a guenon, *Lasiopyga*, with external absence of right thumb. Nos. 6 and 7, infantile coatis, *Ateles*, with anomalous small external thumb on left hand. All after Schultz, 1926b.

FIG. 9

thumb is lacking in adults or at best is but an inconsiderable nailless rudiment, it may be better developed in fetuses. Its extreme stunting, therefore, appears to be of relatively late ontogenetic occurrence (see also Johnston, 1904).

The pollical skeleton always is rudimentary (Fig. 9, no. 3). It comprises a short metacarpal bone and one small phalanx (Flower, Schultz, 1924, 1926b), but a minute second phalanx also can occur (Brooks, 1886). The thumb musculature resembles that of *Ateles*. There is no long flexor tendon (Brooks, Polak) (Fig. 11, E), nor a long extensor (Polak); the long abductor, however, is large (Polak). The short muscles are incompletely differentiated. Both Brooks and Polak noted an adductor and a mass that was inserted as both opponens (to metacarpal) and short flexor (to phalanx). The former investigator also found a short abductor, whereas the latter saw only a sheet of muscle that was inserted not upon bone but upon the thenar skin.

The langur, *Pygathrix* (sive *Semnopithecus*, *Pithecus*), and the proboscis monkey, *Nasalis* (sive *Semnopithecus nasicus*), other members of the sub-family Colobinae, possess thumbs that are comparatively short (Pocock, 1926; Midlo). These are not rudimentary or absent, however, as in *Colobus* (Fig. 8). Yet there is evidence that their musculature also can be incompletely developed. Kohlbrügge (1897) found that the long flexor tendon of the thumb could be replaced by one from the flexor digitorum sublimis (*Pygathrix*), or consist only of a distal, functionless rudiment much as in *Ateles* no. 351 (*Pygathrix*, *Nasalis*), or be completely absent (*Pygathrix*); the other pollical muscles, however, regularly were well-developed.

Truly rudimentary thumbs do not normally occur in catarrhine monkeys of the sub-family Lasiopyginae. Apparently the sole example of such a condition is the specimen of *Lasiopyga pygerythra* described by Schultz (1926b); but this (Fig. 9, no. 5), being completely anomalous, lies outside the scope of this paper.

Pongidae (Great anthropoid apes). On a purely dimensional basis, the thumbs of the three great anthropoid apes—orang-utan, chimpanzee, gorilla—do not fall into the category of rudimentary or stunted digits (Fig. 10). It is true that the evolutionary atrophy of the great ape thumb often has been stressed (see, e.g., Ashley-Montagu, 1931,

and LeGros Clark, 1934). Schultz (1936), however, denied this allegation. He pointed out that the brevity of the pollex in the three large anthropoids is more apparent than real, being due to the great length of the rest of the hand: for when the

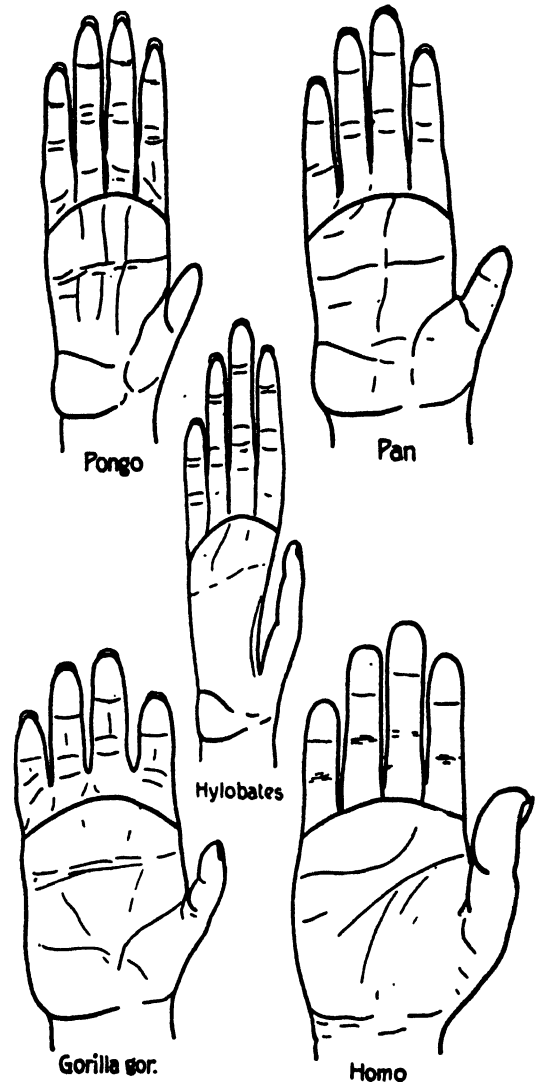


FIG. 10. RIGHT HANDS OF ORANG-UTAN (PONGO), CHIMPANZEE (PAN), GIBBON (HYLOBATES), GORILLA (GORILLA GOR.) AND MAN (HOMO). ALL AFTER MIDLO

ape thumbs are expressed in relation to body size, as represented by length of trunk, their relative lengths do not suffer significantly when compared with that of man.

When we turn to the thumb musculature, however, a stunting clearly is apparent. The follow-

ing account is based partly upon my own dissections of 5 chimpanzees (J. H. Anat. nos. 38, 156, 191, 319, 372), 2 gorillas ("H", from Museum of Comparative Zoology, Harvard University, by courtesy of Mr. H. J. Coolidge, Jr.; and "J", by kindness of Dr. J. F. Fulton of Yale University), and 1 orang-utan (U. S. National Museum no. 153,825), and partly upon the literature. The extensor musculature of my specimens (excepting only gorilla "J") already has been described elsewhere (Straus, 1941).

The most striking muscular deficiency of the thumb in the three great apes relates to its long flexor tendon (Fig. 11, F-H). Of 47 chimpanzees (Beddard; Bischoff, 1870; Boas; Broca (2 animals); Brooks, 1888; Champneys; Chapman, 1879; Duvernoy; Dwight; Embleton; Fick, 1925 (2); Forster, 1917; Gratiolet and Alix; Hartmann; Hepburn; Humphry (2); Huxley, 1864b; Kajava, 1910; Macalister, 1871 and 1874 (2); MacDowell; Michaelis; Schreiber (5); Sonntag, 1923; Sperino; C. Stewart (2); T. D. Stewart; Sutton; Symington; Testut, 1883; Traill; Vrolik; Wilder; Wyman; W. L. S. (5)), this tendon was completely absent (Fig. 11, H) in 30 per cent (14 of 47), a functionless rudiment (Fig. 11, G) in 22 per cent (10½/47), and entirely developed in direct functional continuity with the radial muscle belly of the flexor digitorum profundus (Fig. 11, F) in 48 per cent (22½/47). Among 16 gorillas (Bischoff, 1880; Chapman, 1878; Deniker (2); Duvernoy; Hartmann; Hepburn; Huxley, 1864b; Macalister, 1874; Owen; Pira; Sommer; T. D. Stewart; Symington; W. L. S. (2)), it was lacking in 31 per cent (5/16), rudimentary and inutile in 41 per cent (6½/16), and wholly present in 28 per cent (4½/16). Finally, among 27 orang-utans (Barnard; Beddard; Bischoff, 1870 and 1880 (2); Boas; Brooks, 1888; Chapman, 1880; Church; Duvernoy; Fick, 1895a and 1895b (2); Forster, 1917; Gratiolet and Alix; Hartmann; Hepburn; Huxley, 1864b; Kajava, 1910; Langer; Michaelis; Primrose; Sonntag, 1924; C. Stewart; T. D. Stewart; Sullivan and Osgood; Testut, 1883; Wood; W. L. S.), the tendon was entirely absent in 89 per cent (24/27), rudimentary and functionless in 7 per cent (2/27), and completely developed in but 4 per cent (1/27). Thus the long flexor tendon of the thumb normally is eliminated physiologically in two of the three genera of great apes (96 per cent of oranges, 72 per cent of gorillas) and is entirely without function in fully half the members of the third genus

(52 per cent of chimpanzees). This is a deficiency approaching that of *Ateles* and *Colobus*. Consequently, in a majority of the great anthropoids there is no apparatus for independent flexion of the terminal phalanx of the thumb, although that bone always is developed. A weak, inefficient substitute occasionally is provided by a slender tendinous slip from one of the short thumb muscles, which has been regarded by some investigators (as Langer) as a vestige of the long flexor tendon. Such homology is extremely improbable, however, for this slip can co-exist with the undoubted long pollical tendon (as in my gorilla "H"). Even when a complete, effective long flexor tendon occurs, it almost invariably is described as extremely slender and weak, attesting to its physiological infirmity.

In my animals, the tendon was entirely suppressed in the orang-utan and two of the chimpanzees (nos. 191 and 372). In two other chimpanzees (nos. 156 and 319) and gorilla "J", there was, as in *Ateles* no. 351, a slender, distal, tendinous rudiment in all respects divorced from the fibers of the flexor digitorum profundus but attached distally to the terminal phalanx of the thumb in the manner of a normal tendon: (1) in no. 156, this rudiment arose proximally in two parts—as a thread from the fascial sheath covering the volar aspect of the index finger tendon well above the wrist, and from the dorsal aspect of the transverse carpal ligament radially; (2) in no. 319, it was prolonged from the fascia over the volar base of the first metacarpal bone; and (3) in "J", it developed from the fascia of the wrist deep to the radial part of the flexor digitorum profundus. The incomplete tendon of the fifth chimpanzee (no. 38) differed in that, while filamentous, it was connected proximally not only with the carpal fascia but also apparently with the deep long flexor tendon to the index finger; but it ended short of its expected insertion, in the fascia immediately volar to the metacarpo-phalangeal joint of the thumb. Of my gorilla "H", only the hand, severed at the wrist, was available for study. This exhibited a distinct long flexor tendon of the thumb, attached to the terminal phalanx; there seems but little doubt, moreover, in view of its form and extent, that this tendon was a functional part of the flexor digitorum profundus. The tendinous rudiments of those anthropoid apes that have been described in the literature also regularly assumed the character of distal strands

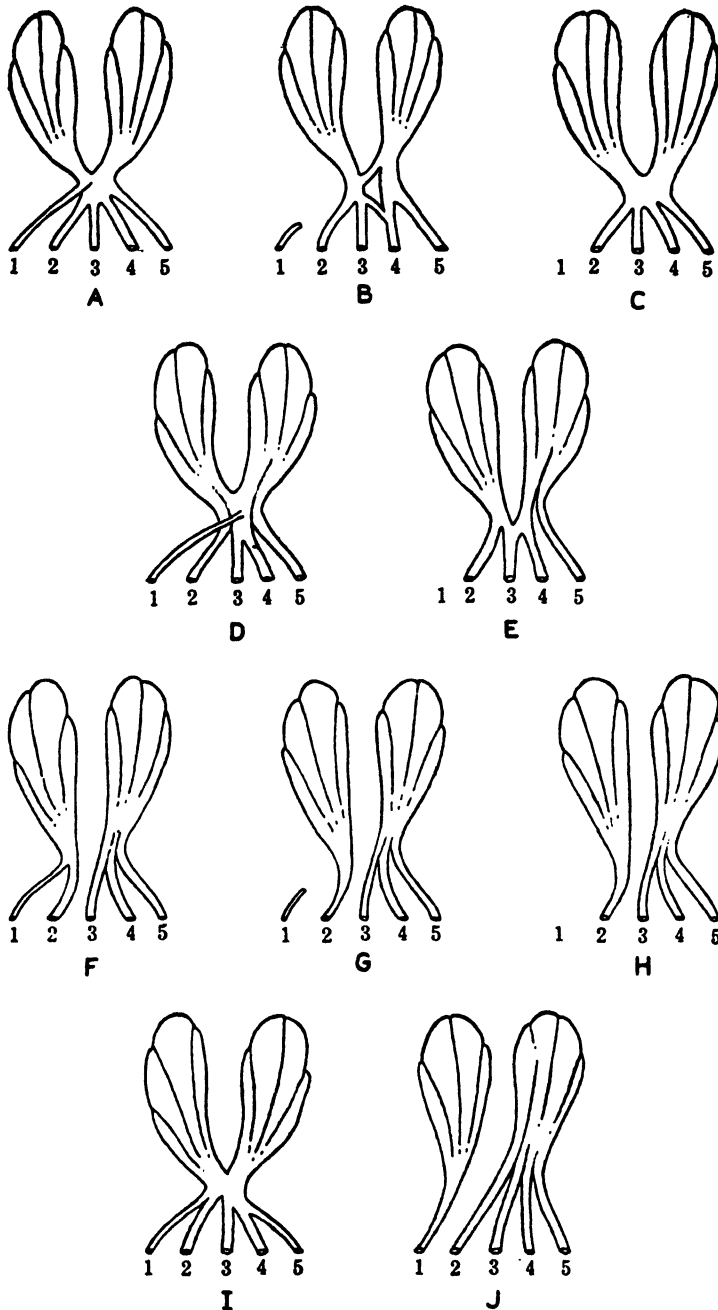


FIG. 11. DIAGRAMS OF THE DEEP LONG FLEXOR MUSCLE OF THE FINGERS (FLEXOR DIGITORUM PROFUNDUS) IN VARIOUS PRIMATES

A, *Cebus* (a representative platyrrhine monkey, for comparison with *Ateles*); B, *Ateles* no. 351; C, *Ateles* no. 47; D, *Macaca* (a representative catarrhine monkey, for comparison with *Colobus*); E, *Colobus* (from data by Polak); F-H, Great anthropoid apes (orang-utan, chimpanzee, gorilla), showing three types of arrangement common to all three animals; I, *Hylobates*; J, Man. This illustration is designed especially to show the enfeebled state or absence of the tendon to the thumb in *Ateles*, *Colobus* and the three great apes. The radial head of the muscle is to the left in each diagram, the ulnar portion to the right. The humeral heads of origin are not shown; there usually is one such head, a so-called condylo-radialis joining the radial portion of the muscle, in all of the above animals save the three great apes.

basically similar to those detailed above. The arrangement noted in my chimpanzee no. 38, however, appears to be essentially unique.

The other thumb muscles customary in primates also normally are present in the great apes, although there is evidence of a decided tendency toward weak or even imperfect development. Of the dorsal muscles, the long abductor alone is regularly powerful as in other primates. An extensor pollicis longus always occurs, but is quite variable in strength—thus I found it to be very robust in a gorilla ("J") and very slender in a chimpanzee (no. 319). Kohlbrügge (1897), indeed, concluded that this muscle is weaker in all of the great anthropoids than it is in man. Some sort of extensor pollicis brevis is not rare in the gorilla—including my specimen "J", in which it was lacking, it has been found in 53 per cent (9 of 17 animals)—and possibly has been seen in one chimpanzee; but it never has been noted in an orang-utan (for details, see Straus, 1941). But since this muscle is an evolutionary novelty, regularly occurring only in man, its deficiency in the large anthropoids is not of the same nature as that involving the long pollical flexor.

Of the five short volar muscles of the thumb, the adductor alone exhibits constant powerful development in all three genera. Indeed, it is their outstanding pollical muscle. Insertion frequently is upon the metacarpal bone (to form the so-called "adductor opponens", physiologically a misnomer) as well as upon the first phalanx—an arrangement otherwise rare in primates, excepting the gibbons. The remaining muscles, however, tend to be comparatively unsubstantial. In fact, in my gorilla "H" the short abductor and the superficial short flexor were much smaller than the corresponding hypothenar muscles; and in gorilla "J" the short abductor was the smallest of the marginal manual muscles. The short abductor also can be poorly developed in the chimpanzee (W. L. S.: no. 319). The superficial short flexor can be an almost tenuous slip (W. L. S.: gorilla "H") or even completely absent (chimpanzee: Michaelis, Duvernoy?); it often is extensively fused with the opponens in gorillas. A true, muscular, deep short flexor of the thumb (*interosseus volaris primus* of Henle) is rare in both the gorilla (apparently found only by Huxley, 1864b) and the chimpanzee (described by Sonntag, 1923; of doubtful homology in my no. 319), but is not uncommon in the orang-utan (Brooks, 1888; Forster, 1917; Primrose; Sullivan and Osgood;

W. L. S.). This muscle, however, is of sporadic occurrence among primates in general, possibly being a normal structure in man alone. The opponens pollicis is extremely variable. In some animals it can be quite robust (gorilla: W. L. S. "H"; chimpanzee: Fick, 1925, W. L. S. nos. 38, 156, 372; orang: Sonntag, 1924), whereas in others it is relatively small or weak (gorilla: W. L. S.: "J"; chimpanzee: Gratiolet and Alix; orang: Brooks, 1888, Church, Duckworth, W. L. S.). Indeed, it can be entirely absent in the chimpanzee, and this apparently not infrequently (Embleton, Traill, Duvernoy?, Forster, 1917?). Keith (1899) declared that this muscle is better marked in the gorilla than in the chimpanzee. According to various authors, it is inclined to be weaker in all three great apes than it is in man (cf. Kohlbrügge, 1897). The opponens pollicis tends to be well-developed in all other Anthropoidea with truly opposable thumbs, namely, catarrhine monkeys, gibbons and man. Hence its proclivity toward weakness or even complete suppression in great apes definitely is a species of stunting consonant with other characteristics of their thumb musculature.

DISCUSSION

From the data presented above, it is clear that stunted or rudimentary digits normally occur on the hands and feet of certain primates. In some genera, either the upper or lower extremity alone is affected in various degrees. In the Lorisidae and the orang-utan, however, the identical digits of both manus and pes are implicated. On the whole, such dwarfing is more advanced in the hand, although in man the fifth toe alone is involved, while the hallux of the orang is even more arrested than the thumb. The latter member, indeed, is more disposed toward defective development than any other finger or toe, at least in the Anthropoidea.

There appears to be no absolute correlation between skeleton and musculature. In some instances the skeleton is the more severely curtailed (fifth toe of man, hallux of orang), in others the musculature (thumbs of great apes and of *Pygathrix* and *Nasalis*), while in still others both bones and muscles show approximately the same degrees of abridgment (second toes and second fingers of Lorisidae, thumbs of *Ateles* and *Colobus*). The nail is absent only when the skeleton is extremely abbreviated.

The long, extrinsic muscles of the affected digit,

whether finger or toe, definitely tend to be more defective than the short, intrinsic muscles. This is especially apparent when the digit is truly rudimentary, as in the hallux of the orang-utan, the index finger of *Perodicticus*, and the thumbs of *Ateles* and *Colobus*. The same tendency, moreover, also is evident in less reduced digits.

The significance of normally dwarfed or rudimentary digits is not entirely apparent. What factors might be operating to so affect the fifth toe of man and the hallux of the orang-utan are a complete mystery. There is a possible functional correlation, however, for the arrested second digits of both hand and foot of the Lorisidae. In these animals, the powerfully developed thumb and hallux both are set apart from the other digits so as to produce veritable pincers (see Forster, 1933b, who has discussed this subject in great detail). The normal abduction of thumb and hallux is so pronounced that neither can be as completely adducted as in other primates (Figs. 1 and 2). Of the ulnar (or fibular) prong of the pincers, the fourth finger (or toe) is predominant and is the podial axis—as witness its relatively great length and the arrangement of the short manual (or pedal) muscles, notably the interossei, about it. Incidentally, this disposition toward predominance of the fourth digit and an associated grouping of the musculature is a distinct lemurine feature more or less characteristic of the Lemuroidea as a whole (see Straus, 1930, a and b). Elimination or even reduction of the digits intervening between it and the first would tend to increase the span of the pincers, but scarcely, it would seem, without decreasing the strength of its grasp. In this connection, it seems significant that Hill (1936) has indicated a dwarfing of not only the second digits but also of the third in some Lorisidae.

When we come to consider the thumb, there appears to be a distinct relation between its stunting and the habit of bimanual arboreal locomotion or "brachiation." For the chimpanzee and orang-utan, the Colobinae (see Pocock, 1926), and the Atelinae all are accomplished brachiators. The gorilla, chiefly because of the limitations imposed by its great adult weight, is a brachiator only in immaturity; but there is little doubt of its definite brachiating ancestry. Furthermore, it will be obvious to those who have observed living primates that brachiation fundamentally is dependent upon only the four ulnar fingers. The thumb not only is not involved, but actually can

be an incumbrance, for a forceps- or pincers-like grasp is not employed. It is not illogical, therefore, to assume a correlation between dwarfing of the thumb and the habit of brachiation in Atelinae, Colobinae and great anthropoid apes.

It nevertheless is certain that a stunted pollex is not an inevitable accompaniment of a brachiating method of locomotion. For the Hylobatidae—gibbons and siamang—are extraordinary and habitual brachiators, far surpassing the great apes, yet they give no evidence of pollical deficiency. In these animals (Fig. 10), the thumb is of relatively great length, even being somewhat longer, comparatively, than that of man, especially in *Hylobates* (Schultz, 1936). Its musculature, although uniquely specialized in some respects—as in the marked tendency for its short muscles to be powerfully inserted upon the metacarpal bone—in no sense is defective or weak. Thus, for example, a well-developed long flexor tendon of the thumb was present and completely functional in all of 13 specimens that have been reported upon (Bischoff, 1870; Chapman, 1901; Deniker; Hartmann; Hepburn; Huxley, 1864b; Kohlbrügge, 1890 (3); C. Stewart; W. L. S. (3)). Perhaps this compatibility of a well-developed thumb with constant brachiation can be traced to the mode of bimanual locomotion peculiar to gibbons and siamangs. Their thumb is separated from the other fingers by a great cleft that uniquely extends far proximal to the first metacarpo-phalangeal joint (Fig. 10); hence the pollex, despite its great length, easily can be bent across the proximal palm, where it is of no hindrance in brachiation. Or, on occasion, the thumb can be tucked away, so as virtually to be flush with the palm, in the peculiar groove along the radial side of the hand that is found only in Hylobatidae (also see Pocock, 1926). These are not the only peculiarities of gibbons that probably are related to their type of brachiation. For they possess certain muscular specializations of the upper extremity not encountered in the three great anthropoids, *Colobus* and *Ateles*. As indicated in an earlier paper (Straus, 1940), the term "brachiation" is a broad one, for the mode of bimanual arboreal locomotion is not precisely identical in all "brachiators," and adaptations to such form of progression have been made in different ways.

From an evolutionary aspect, the underdevelopment and functional weakness of the thumb in the three great apes is a regression. The comparatively feeble nature of this digit will be well

appreciated by those who have had experience with living anthropoids. On the other hand, the thumb relatively is much stronger in most catarrhine monkeys (save the Colobinae), Hylobatidae and man. In fact, the remarkable development of the human thumb, especially of its associated musculature, contrasts strikingly with the conditions in the great anthropoid apes. There is not the slightest evidence of an evolutionary degeneration in the structure of man's thumb. Thus, functional default of its long flexor tendon, so common in the great apes, is among the rarest of all human muscular anomalies. To my knowledge, it has been reported for but five bodies, all white—by Gegenbaur (1861), Wagstaffe (1872), Gruber (1875), Chudzinski (1881), and Fromont (1895). Of these, the tendon was entirely lacking in two, present in the other three in the form of a distal rudiment as in many examples of the giant anthropoids. At least two of these bodies, however, possessed other, associated muscular anomalies and even serious defects, while the third was that of a microcephalic infant. Hence these instances appear to have no more phylogenetic significance than other anomalies of a similar nature. The constancy of the long flexor tendon of the human thumb is indicated by the fact that both Testut (1883) and Le Double (1897) found it always present in over 200 and in 327 French bodies, respectively. Furthermore, I myself never have noted its absence nor deficiency, nor have I ever been apprised of such condition during my fifteen years in this laboratory, although fully 300 cadavers, chiefly Negro, have passed through the dissecting rooms during that time.

Thus it is clear that a comparative study of the thumb yields additional evidence in support of the view, expressed in previous papers (Straus, 1940, 1941), that man did not pass through a pronounced "brachiating" stage in his phylogeny: for the human thumb essentially is of a generalized structure, completely lacking not only the defective qualities found in the pollices of the great apes and most other brachiators but also the peculiar specializations relating to the thumbs of the Hylobatidae. This evidence likewise presents a major obstacle for those who believe that man has other than a very remote relationship to the great apes.

SUMMARY

The Primates in general are characterized by five well-developed digits on both manus and pes.

A few forms, nevertheless, normally possess one or more stunted or rudimentary digits. These forms include the lorissine lemurs (second finger and second toe), the platyrrhine Atelinae (thumb), the catarrhine Colobinae, particularly *Colobus* (thumb), the orang-utan (thumb and hallux), the chimpanzee (thumb), the gorilla (thumb), and man (fifth toe).

There appears to be no absolute correlation between bones and muscles. In some rudimentary digits the skeleton is the more severely affected (fifth toe of man, hallux of orang), in others the musculature (thumbs of great apes and of certain Colobinae), while in still others both of these structures exhibit essentially similar degrees of curtailment (second fingers and toes of Lorisidae, thumbs of *Ateles* and *Colobus*). The long, extrinsic muscles of the affected digit distinctly tend to be more defective than the short, intrinsic muscles.

The significance of some normally rudimentary digits (fifth toe of man, hallux of orang) is entirely obscure. The arrested digits of the Lorisidae, however, seem to be related to the peculiar pincers-like grasp of their hands and feet, in which the first and fourth are the dominant digits. As for a rudimentary or stunted thumb, this apparently can be correlated with the habit of "brachiation." This mode of locomotion, nevertheless, is not necessarily accompanied by a poorly-developed thumb, as witness the Hylobatidae. These animals clearly are adapted to a brachiating life in a manner quite different from that of Atelinae, Colobinae, and great apes.

The evidence produced by a comparative study of the thumb supports not only the view that man's phylogeny did not include a pronounced brachiating stage, but also that view which denies man other than very remote relationship to the great anthropoid apes.

LIST OF LITERATURE

- ADACHI, B. 1905. Die Fussknochen der Japaner. *Mitt. Med. Fak. Kais.-Jap. Univ. Tokyo*, 6:307-344.
- ASHLEY-MONTAGU, F. M. 1931. On the Primate thumb. *Amer. J. Phys. Anthropol.*, 15: 291-314.
- BARNARD, W. S. 1875. Observations on the membral musculature of *Simia satyrus* (Orang) and the comparative myology of man and the apes. *Proc. Amer. Ass. Adv. Sci.*, 112-144.
- BEDDARD, F. E. 1893. Contributions to the anatomy of the anthropoid apes. *Trans. Zool. Soc. Lond.*, 13: 177-218.
- BISCHOFF, T. L. W. VON. 1870. Beiträge zur Anatomie des *Hylobates leuciscus* und zu einer ver-

- gleichenden Anatomie der Muskeln der Affen und des Menschen. *Abh. Kön. Bayer. Akad. Wiss., Math.-Phys. Cl.*, 10 (3): 197-297.
- . 1880. Beiträge zur Anatomie des Gorilla. *Abh. Kön. Bayer. Akad. Wiss., Math.-Phys. Cl.*, 13 (3): 1-48.
- BOAS, J. E. V. 1919. Einige Bemerkungen über die Hand des Menschen. *Kgl. Dan. Videnskab. Selskab, Biol. Medd.*, 2 (1): 32 pp.
- BOYER, ESTHER L. 1935. The musculature of the inferior extremity of the orang-utan, *Simia satyrus*. *Amer. J. Anat.*, 56: 193-256.
- BROCA, P. 1869. L'ordre des Primates. *Bull. Soc. Anthropol. Paris*, ser. 2, 4: 228-401.
- BROOKS, H. ST. JOHN. 1886. On the morphology of the intrinsic muscles of the little finger, with some observations on the ulnar head of the short flexor of the thumb. *J. Anat. Physiol., Lond.*, 20: 645-661.
- . 1888. On the short muscles of the pollex and hallux of the anthropoid apes, with special reference to the opponens hallucis. *J. Anat. Physiol., Lond.*, 22: 78-95.
- CHAMPNEYS, F. 1872. On the muscles and nerves of a chimpanzee (*Troglodytes niger*) and of a *Cynocephalus anubis*. *J. Anat. Physiol., Lond.*, 6: 176-211.
- CHAPMAN, H. C. 1878. On the structure of the gorilla. *Proc. Acad. Nat. Sci. Phila.*, 385-394.
- . 1879. On the structure of the chimpanzee. *Proc. Acad. Nat. Sci. Phila.*, 51-63.
- . 1880. On the structure of the orang outang. *Proc. Acad. Nat. Sci. Phila.*, 1-16.
- . 1901. Observations upon the anatomy of *Hyllobates leuciscus* and *Chiromys madagascariensis*. *Proc. Acad. Nat. Sci. Phila.*, 414-423.
- CHUDZINSKI, T. 1881. Anomalies régressives des muscles fléchisseurs profonds de la main chez une jeune fille microcéphale. *Bull. Soc. Anthropol. Paris*, 279-284. (Cited by Le Double, Sommer, Testut, 1883.)
- CHURCH, W. S. 1861 and 1862. On the myology of the orang utang (*Simia Morio*). *Nat. Hist. Rev.*, 510-516 (1861); 82-94 (1862).
- CLARK, W. E. LE GROS. 1934. Early Forerunners of Man. *London: Ballière, Tindall & Cox.*
- DENIKER, J. 1886. Recherches anatomiques et embryologiques sur les singes anthropoïdes. Thèse Sci., Paris. *Poitiers: Typographie Oudin.*
- DUCKWORTH, W. L. H. 1904. Dissections of the upper limb of *Gorilla*, *Hyllobates* and *Cynocephalus*. *Stud. Anthropol. Lab., Anat. Sch., Cambridge*, no. 16: 91-97.
- DUVERNOY, G. L. 1855-56. Des caractères anatomiques des grands singes pseudo-anthropomorphes. *Arch. Mus. Hist. Nat. Paris*, 8: 1-248.
- DWIGHT, T. 1895. Notes on the dissection and brain of the chimpanzee "Gumbo" (*Troglodytes niger*). *Mem. Boston Soc. Nat. Hist.*, 5: 31-52.
- ELLIOT, D. G. 1913. A Review of the Primates. 3 vols., *New York: Amer. Mus. Nat. Hist.*
- ELZE, C. 1910. Ueber die Gelenkhöhle am distalen Ende des Daumenrudimentes von *Ateles ater*. *Anat. Anz.*, 37: 543-544.
- EMBLETON, D. 1864. Notes on certain parts of the anatomy of a young chimpanzee. *Nat. Hist. Rev.*, 4: 250-258.
- FICK, R. 1895a. Vergleichend anatomische Studien an einem erwachsenen Orang-Utang. *Arch. Anat. Physiol., Anat. Abt.*, 1-96.
- . 1895b. Beobachtungen an einem zweiten erwachsenen Orang-Utang und einem Schimpanse. *Arch. Anat. Physiol., Anat. Abt.*, 289-318.
- . 1925. Beobachtungen an den Muskeln einiger Schimpansen. *Z. Anat. EntwickGesch.*, 76: 117-141.
- FLOWER, W. H. 1885. An Introduction to the Osteology of the Mammalia. 3rd edit., *London: Macmillan & Co.*
- FORSTER, A. 1917. Die Mm. contrahentes und interossei manus in der Säugetierreihe und beim Menschen. *Arch. Anat. Physiol., Anat. Abt.*, 101-378.
- . 1933a. Contribution à l'évolution du pouce. III. Chez *Perodicticus potto*. *Arch. Anat. Histol. Embryol.*, 16: 339-355.
- . 1933b. La "pince palmaire" et la "pince plantaire" de *Perodicticus potto*. *Arch. Anat. Histol. Embryol.*, 17: 181-246.
- FROMONT. 1895. Anomalies musculaires multiples de la main. Absence du fléchisseur propre du pouce. Absence des muscles de l'éminence thénar. Lombricaux supplémentaires. *Bull. Soc. Anat. Paris*, ser. 5, 9: 395-401.
- GEGENBAUR, C. 1861. Ein Fall von Muskelanomalien an der oberen Extremität. *Arch. Path. Anat. Physiol. Klin. Med. (Virchow)*, 21: 376-385.
- GLAESMER, ERNA. 1910. Die Beugemuskeln am Unterschenkel und Fuss bei den Marsupialia, Insectivora, Edentata, Prosimiae und Simiae. *Morph. Jb.*, 41: 149-336.
- GRATIOLET, L. P., AND P. H. E. ALIX. 1866. Recherches sur l'anatomie du *Troglodytes Aubryi*, chimpanze d'une espèce nouvelle. *Nouv. Arch. Mus. Hist. Nat. Paris*, 2: 1-264.
- GRUBER, W. 1875. Ein Fall des Vorkommen des Musculus flexor pollicis longus beim Menschen: als Tensor bursae mucosae tendinum Mm. flexorum, oder als Kopf des M. flexor digitorum profundus manus. *Arch. Anat. Physiol. Wiss. Med.*, 211-214.
- HAFFERL, A. 1929. Bau und Funktion des Affenfusses. I. Die Anthropoiden. *Z. Anat. EntwickGesch.*, 88: 749-783.

- HARTMANN, R. 1886. *Anthropoid Apes*. New York: D. Appleton & Co.
- HASEBE, K. 1912. Über die Häufigkeit der Coalescenzen, Synostosen und Assimilationen der Fussknochen der Japaner und eine neue Coalescenz (*Coalescentia cuneo-navicularis* I). *Z. Morph. Anthropol.*, 14: 495-500.
- HEPBURN, D. 1892. The comparative anatomy of the muscles and nerves of the superior and inferior extremities of the anthropoid apes. *J. Anat. Physiol., Lond.*, 26: 149-186, 324-356.
- HILL, W. C. O. 1936. The affinities of the loroids. *Ceylon J. Sci.*, sect. B, 19: 187-314.
- HUMPHRY. 1867. On some points in the anatomy of the chimpanzee. *J. Anat. Physiol., Lond.*, 1: 254-268.
- HUNTER, R. H. 1925. The extensor muscles of the hinder foot in mammals. *Proc. Zool. Soc. Lond.*, 457-494.
- HUXLEY, T. H. 1864a. On the angwantibo (*Arctocebus calabarensis*, Gray) of Old Calabar. *Proc. Zool. Soc. Lond.*, 314-335.
- . 1864b. The structure and classification of the Mammalia. *Med. Times & Gazette*, vols. I & II for 1864.
- . 1883. *A Manual of the Anatomy of Vertebrated Animals*. New York: D. Appleton & Co.
- JOHNSTON, H. 1904. The Uganda Protectorate. New York. (Quoted by Schultz, 1926b).
- KAJAVA, Y. 1910. Die kurzen Muskeln und die langen Beugemuskeln der Säugetierhand. I. Monotremata und Marsupialia. *Anat. Hefte*, 42: 1-94.
- . 1911. Die kurzen Muskeln der Halbaffenhand. *Voeltzkow, Reise in Ostafrika in den Jahren 1903-1905, Wiss. Ergeb.*, 4: 355-382.
- KEITE, A. 1899. On the chimpanzees and their relationship to the gorilla. *Proc. Zool. Soc. Lond.*, 296-312.
- KOHLBRÜGGE, J. H. F. 1890. Muskeln und periphere Nerven des Genus *Hylobates*. Inaug.-Diss. Med., Univ. Freiburg. *Leiden*.
- . 1897. Muskeln und periphere Nerven der Primaten, mit besonderer Berücksichtigung ihrer Anomalien. *Verh. Kon. Akad. Wet., Amst.*, sect. 2, 5 (6): 246 pp.
- LANGER, C. 1879. Die Musculatur der Extremitäten des Orang als Grundlage vergleichend-myologischen Untersuchung. *S. B. Kais. Akad. Wiss. Wien, Math.-Nat. Cl.*, 79 (3): 177-222.
- LECHE, W. 1874-1900. Säugethiere: Mammalia. Musculatur. *Bronn's Kl. u. Ord. Thier-Reichs*, 6 (5): 649-919.
- LE DOUBLE, A. F. 1897. *Traité des Variations du Système Musculaire de l'Homme et de leur Signification au Point de Vue de l'Anthropologie Zoologique*. 2 vols., Paris: Schleicher Frères.
- MACALISTER, A. 1871. On some points in the myology of the chimpanzee and others of the primates. *Ann. & Mag. Nat. Hist.*, 7: 341-351.
- . 1874. The muscular anatomy of the gorilla. *Proc. Roy. Irish Acad.*, ser. 2, 9: 501-506.
- MACDOWELL, E. C. 1910. Notes on the myology of *Anthropopithecus niger* and *Papio-thoth ibeanus*. *Amer. J. Anat.*, 10: 431-460.
- MACKENZIE, D. W., JR. 1931. The mechanism of the lemurine foot. *Trans. Roy. Soc. Can.*, ser. 3, 25: 45-57.
- MICHAELIS, P. 1903. Beiträge zur vergleichenden Myologie des *Cynocephalus babuin*, *Simia satyrus*, *Troglodytes niger*. *Arch. Anat. Physiol., Anat. Abt.*, 205-256.
- MIDLO, C. 1934. Form of hand and foot in primates. *Amer. J. Phys. Anthropol.*, 19: 337-389.
- MURIE, J., AND ST. G. MIVART. 1872. On the anatomy of the Lemuroidea. *Trans. Zool. Soc. Lond.*, 7: 1-113.
- OWEN, R. 1866. *On the Anatomy of Vertebrates*. 3 vols., London: Longmans, Green & Co.
- PFITZNER, W. 1896. Beiträge zur Kenntnis des menschlichen Extremitätenskeletts. VII. Die Variationen im Aufbau des Fuss skeletts. *Morph. Arb.*, 6: 245-258.
- PIRA, A. 1913. Beiträge zur Anatomie des Gorilla. I. Das Extremitätenmuskelsystem. *Morph. Jb.*, 47: 309-354.
- POCOCK, R. I. 1925. Additional notes on the external characters of some platyrrhine monkeys. *Proc. Zool. Soc. Lond.*, 27-47.
- . 1926. The external characters of the catarrhine monkeys and apes. *Proc. Zool. Soc. Lond.* (1925), 1479-1579.
- POLAK, CLARA. 1908. Die Anatomie des Genus *Colobus*. *Verh. Kon. Akad. Wet., Amst.*, sect. 2, 14 (2): 247 pp.
- PRIMROSE, A. 1900. The anatomy of the orang outang. *Univ. Toronto Stud., Anat. Stud.* No. 1, 94 pp.
- RIBBING, L. 1909. Die Unterschenkel und Fussmuskulatur der Tetrapoden und ihr Verhalten zur der entsprechenden Arm- und Handmuskulatur. *Lunds Univ. Årsskrift, N. F.*, Afd. 2, 4 (5): 158 pp.
- RUGE, G. 1878a. Untersuchung über die Extensorengruppe am Unterschenkel und Fusse der Säugethiere. *Morph. Jb.*, 4: 592-643.
- . 1878b. Zur vergleichenden Anatomie der tiefen Muskeln in der Fusssohle. *Morph. Jb.*, 4: 644-659.
- SAWALISCHIN, MARIE. 1911. Der *Musculus flexor communis brevis digitorum pedis* in der Primatenreihe mit spezieller Berücksichtigung der menschlichen Varietäten. *Morph. Jb.*, 42: 557-663.
- SCHREIBER, H. 1936. Die Extreimbewegung der Schimpansenhand. 2. Mitteilung zu: Zur Mor-

- phologie der Primatenhand. *Morph. Jb.*, 77: 22-60.
- SCHULTZ, A. H. 1924. Observations on *Colobus* fetuses. *Bull. Amer. Mus. Nat. Hist.*, 49: 443-457.
- 1925. Embryological evidence of the evolution of man. *J. Wash. Acad. Sci.*, 15: 247-263.
- 1926a. Variations in man and their evolutionary significance. *Amer. Nat.*, 60: 297-323.
- 1926b. Fetal growth of man and other primates. *QUART. REV. BIOL.*, 1: 465-521.
- 1936. Characters common to higher primates and characters specific for man. *QUART. REV. BIOL.*, 11: 259-283, 425-455.
- 1941. Growth and development of the orang-utan. *Contrib. Embryol.* no. 182, *Carneg. Instn. Wash. Pub.* no. 525: 57-110.
- 1942. Growth and development of the proboscis monkey. *Bull. Mus. Comp. Zool., Harvard*, 89: 287-314.
- SENFT, M. 1907. Myologie der Vorderextremitäten von *Hapale jacchus*, *Cebus macrocephalus* und *Ateles ater*. Inaug.-Diss., Bern.
- SOMMER, A. 1907. Das Muskelsystem des Gorilla. *Jena. Z. Naturwiss.*, 42: 181-308.
- SONNTAG, C. F. 1923. On the anatomy, physiology and pathology of the chimpanzee. *Proc. Zool. Soc. Lond.*, 323-429.
- 1924. On the anatomy, physiology and pathology of the orang-utan. *Proc. Zool. Soc. Lond.*, 349-450.
- SPERINO, G. 1897. Anatomia del cimpanzè (*Aethropopithecus troglodytes* Trouessart) in rapporto con quella degli altri antropoidi e dell'uomo. Torino: Unione tipografica.
- STEWART, C. 1900. Descriptive and Illustrated Catalogue of the Physiological Series of Comparative Anatomy Contained in the Museum of the Royal College of Surgeons of England. Vol. I, 2nd edit., London: Taylor & Francis.
- STEWART, T. D. Letter of February 27, 1936.
- STRAUS, W. L., JR. 1927. Growth of the human foot and its evolutionary significance. *Contrib. Embryol.* no. 101, *Carneg. Instn. Wash. Pub.* no. 380: 93-134.
- 1930a. The foot musculature of the highland gorilla (*Gorilla beringei*). *QUART. REV. BIOL.*, 5: 261-317.
- 1930b. Parallelism in the interosseous muscles of primate hand and foot. *Anat. Rec.*, 45: 279.
- 1940. The posture of the great ape hand in locomotion, and its phylogenetic implications. *Amer. J. Phys. Anthropol.*, 27: 199-207.
- 1941. The phylogeny of the human forearm extensors. *Human Biol.*, 13: 23-50, 203-238.
- SULLIVAN, W. E., AND C. W. OSGOOD. 1927. The musculature of the superior extremity of the orang-utan, *Simia satyrus*. *Anat. Rec.*, 35: 193-239.
- SUTTON, J. B. 1884. On some points in the anatomy of the chimpanzee. *J. Anat. Physiol., Lond.*, 18: 66-85.
- SYMINGTON, J. 1890. Observations on the myology of the gorilla and chimpanzee. *Rep. Brit. Ass. Adv. Sci.* (1889): 629-630.
- TESTUT, L. 1883. Le long fléchisseur propre du pouce chez l'homme et chez les singes. *Bull. Soc. Zool. Fr.*, 8: 164-185.
- 1884. Les Anomalies Musculaires chez l'Homme Expliquées par l'Anatomie Comparée. Paris: G. Masson.
- TRAILL, T. S. 1821. Observations on the anatomy of the orang outang. *Mem. Werner. Nat. Hist. Soc.*, 3: 1-49.
- VAN CAMPEN, F. A. W. 1859. (Anatomy of *Pterodicticus potto*.) *Verh. Kon. Akad. Wet., Amst.* (Cited by Murie and Mivart.)
- VROLIK, W. 1841. Recherches d'Anatomie Comparée sur le Chimpanzé. Amsterdam: Johannes Müller. (Cited by Champneys, Deniker, Le Double, Macalister, Mac Dowell, Sommer, Testut, Wilder.)
- WAGSTAFFE, W. W. 1872. Partial deficiency of the tendon of the long flexor of the thumb. *J. Anat. Physiol., Lond.*, 6: 212-214.
- WELLS, L. H. 1935. A peroneus tertius muscle in a chacma baboon (*Papio porcarius*). *J. Anat., Lond.*, 69: 508-514.
- WILDER, B. G. 1861. Contributions to the comparative myology of the chimpanzee. *Boston J. Nat. Hist.*, 7: 353-384.
- WOOD, J. 1867. Variations in human myology observed during the winter session of 1866-67 at King's College, London. *Proc. Roy. Soc. Lond.*, 15: 518-546.
- WOOD JONES, F. 1918. Arboreal Man. London: Edward Arnold.
- WYMAN, J. 1855. (Chimpanzee.) *Proc. Boston Soc. Nat. Hist.*, 5. (Cited by Deniker, Le Double, Macalister, Testut.)
- YERKES, R. M., AND ADA W. YERKES. 1929. The Great Apes. New Haven: Yale Univ. Press.



ON THE INTERPRETATION OF RADIATION EXPERIMENTS IN GENETICS

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AN INTERPRETATION of the X-ray production of mutations has been formulated on the basis of the "hit theory" or "target hypothesis" (see especially Timofeeff-Ressovski, 1937; further developments by Lea, 1940). The theory assumes that a "gene mutation" is produced by ionizing radiations whenever some primary phenomenon, a "hit," occurs within a certain region of space called the "target." Although the theory successfully accounts for several important experimental facts, it is subject to criticism. Some progress has already been made towards less specific but also less restrictive interpretations of the experimental data (e.g. Muller, 1940). It is the purpose of the present paper to consider again the implications of the experimental data in an effort to show which results of the hit theory are independent of its binding assumptions. Certain types of mutations, for instance the "gene mutations," have been frequently considered in the literature on the hit theory as well defined and homogenous classes of phenomena. The same procedure will be followed for simplicity in this paper, while its possible criticism is considered in another paper (Fano, 1941).

1. The interpretation according to the hit theory

Ionizations distributed according to probability laws have generally been considered as the primary physical phenomena leading to the random production of mutations. The target might be identical with the gene, but may conceivably be larger or smaller; it might consist of many parts.

On the basis of random distribution of ionizations within irradiated matter, the probability of producing an ionization within the target, and hence the frequency of mutations, must be proportional to the total number of ionizations produced. The following well-known results of X-ray experiments can then easily be explained:

(a) The number of gene mutations produced in N_0 *Drosophila* sperms by the dose D of X- or γ -rays is proportional to both N_0 and D :

$$N = \text{const. } N_0 D \quad \bullet (1)$$

(b) The constant is independent of variations in wave-length and in the time distribution of irradiation, if the radiation dosage is measured as any equivalent of the ionization produced per unit volume of matter.

The frequency of ionizations within the target is given by the size of the target times the number of ionizations per unit volume. Therefore, the size of the target can be calculated according to the hit theory from the experimental value of the constant in formula (1). In experiments on single mutations the target has been found to be about $1 \text{ m}\mu$ in size, that is to contain about 1000 atoms.

The efficiency of radiation should be reduced by an excessive density of ionizations. The ionizations produced by radiations are not distributed fully at random but lie along the path of "ionizing particles." When the distance of successive ionizations is smaller than the thickness of the target, a single ionizing particle may produce several ionizations within the target. The actions of these ionizations do not add up, because each one of them is sufficient to produce a mutation, and thus there arises a waste of ionizations. Hence the number of mutations produced by a given number of ionizations should be smaller than in the case of radiation with a low density of ionization. This phenomenon is called "saturation effect."

Investigations with soft X-rays producing densely ionizing photoelectrons failed to show any saturation effect on gene mutations in *Drosophila* (Wilhelmy, Zimmer and Timofeeff-Ressovski, 1936; Fricke and Demerec, 1937). Jordan (1938a) pointed out that Wyckoff's data (1930) on the killing of *Escherichia coli* by soft X-rays show the beginning of a saturation effect. The thickness of

the target for the killing of *E. coli* should thus be approximately equal to the average distance of ionizations in the experiment ($\approx 6 \mu$). Zimmer and Timofeeff-Ressovski (1938) found a saturation effect in the production of sex-linked lethals in *Drosophila melanogaster* by neutron rays, which act through densely ionizing protons. The production of lethals by neutrons follows formula (1) but the constant factor is 1.6 times smaller than in the case of X-rays. Investigations by Gray and Read, 1939, confirm the reliability of the dosimetry used by Zimmer, 1938, and thus support the results of the neutron experiment.

A quantitative theory of the saturation effect was developed by Lea (1940) who calculated the dependence of the constant in formula (1) upon the ion density, in the case of a spherical target. Lea assumed that the target for sex-linked lethals consists of a number of spherical targets each of them corresponding to a locus of the X-chromosome where the lethal may occur. The total volume of the targets is given by the X-ray experiments; the average thickness of the single "targets" is given by the neutron experiment and the theory of the saturation effect. Hence Lea deduced that the target for all sex-linked lethals consists of about 1860 spheres. This number represents also the total number of genes in the X-chromosome, if the further assumption is made that each gene is capable of exhibiting a lethal mutation. The single spherical targets are found to be of the same order of magnitude as the targets for individual visible mutations of single genes; this coincidence lends further support to the theory. Thus Lea's estimate of the "number of genes" might also be deduced as the ratio of the frequency of all sex-linked lethals to the frequency of individual mutations.

2. Discussion on the size of the target

The broadest principle of the hit theory is that the statistical law:

$$N = kN_0D, \quad (k = \text{constant}), \quad (1)$$

is determined by inherent characteristics of the biophysical process. (N is the average number of mutations, N_0 the number of irradiated sperms, D the dose. Which class of mutations is considered is immaterial here.) While the constant k is defined experimentally as the average frequency of mutations produced by unit dose, according to

the hit theory it must have some particular theoretical meaning. An initial set of assumptions which have been widely accepted is then required:

(a) The observed discontinuous mutation phenomena correspond to an actual "all or none" primary phenomenon in the genetic material.

(b) The genetic material of different sperms may be considered as identical.

(c) The experimental law (1) is valid beyond the present stage of investigation, i.e. it is valid down to any low dosage and there is no dependence whatsoever on the time distribution of irradiation.

If (a), (b), and (c) are fulfilled, k may be interpreted as the *mathematical probability* that one unit radiation dose produces a mutation in any particular sperm. The choice of the unit of dosage is thus far arbitrary but different numerical values of k correspond to different units.

It is interesting to consider units of dosage emphasizing the discontinuous nature of radiation. The unit of dosage may be related to a "flow" of radiation (for example the passage of one X-ray quantum or of one particle per sq. cm.) or to the production of secondary phenomena within matter (for example the production of one ionization or of one secondary electron per cc.). In the first case the probability k is equal to the area of a surface which is crossed by a quantum as frequently as a mutation is produced, in the second case it is equal to the volume of a region within which one secondary phenomenon is produced with the same frequency. An area or volume equal to k will then represent the probability of production of a mutation and is accordingly called an "effective cross section" or an "effective volume." In order to follow the familiar procedure, the production of one ionization per cc. at a random position within matter will be assumed as a unit of dosage throughout this section. This unit is a definite fraction,

$$1/(2 \times 10^{12})$$

of the roentgen unit. The reasons for this choice and its actual significance will be discussed in the following sections. Then k shall represent the "effective volume" for the production of a mutation (of the class under consideration) by an ionization and will be indicated by τ .

An experiment may be considered as a numerical example, in which 591 CLB tests for sex-linked lethals were carried out among the offspring of *Drosophila* males X-rayed with 4500 r and 72 lethals were found. The following figures must

then be entered in formula (1): $N = 72$, $N_0 = 591$, $D = 4500 \times 2 \times 10^{13}$ ionizations/cm.³; hence

$$\tau = k = \frac{72}{591 \times 4500 \times 2 \times 10^{13}} \approx 10^{-17} \text{ cm.}^3$$

The hit theory further assumes usually that the "effective volume" τ defined above is not simply a probability, i.e. a mathematical quantity, but that it measures the actual volume of a target. This assumption goes far beyond the preceding ones. It does not seem necessarily correct to assume that τ measures an actual volume. On one hand there certainly is a relationship between τ and an actual volume, because an ionization can be effective only if it occurs sufficiently close to the place of production of a mutation, i.e. within some specific "sensitive region." This relationship may be called a *spatial probability factor*. There is, however, another factor affecting the value of τ , which has been taken into consideration only recently (e.g. Jordan, 1939; Muller, 1940) and which may be called the *physical probability factor*. Whenever an atomic system absorbs an amount of energy, for instance through an ionization, the outcome of the phenomenon is not completely determined. Thus a free excited atom can emit alternately light of different colors; atomic mechanics can determine only the relative probability of different emissions. Whenever a molecule is supplied with the activation energy required for a certain reaction, the reaction does not necessarily occur; its probability is frequently called "quantum efficiency" and it may approach one, or it may be very small. Only a detailed knowledge of the reaction and of the structure of the atomic system which is affected can afford an *a priori* evaluation of the physical probability factor. It is quite possible, moreover, that there is no immediate strictly physical connection between the physical phenomena produced by radiation and the change of the genetic material which is a mutation. Ionizations or analogous phenomena might act primarily as a perturbation to the biochemical system of which the genetical material is a part; a further chain of physico-chemical processes might or might not, according to chance, lead to a mutation (see, e.g. Fricke and Demerec, 1937).

The "effective volume" τ should then be split into a factor V representing the spatial factor, i.e. the actual volume of a sensitive region, and a physical factor p , i.e. the average probability that an

ionization occurring within the sensitive region produces a mutation ($\tau = pV$). No satisfactory method has yet been developed to evaluate even the order of magnitude of p and V separately. The only present possibility of evaluating directly the size of the "sensitive volume" might be offered by the saturation effect (Section 4). A purely physical approach to the same problem is to consider the maximum distance of propagation of the physical atomic actions arising from an ionization as the radius of the sensitive region; the sensitive region would thus be introduced as a theoretical physical quantity. It is difficult, however, to draw conclusions along this line without any detailed knowledge of the atomic structure of the matter involved. When special circumstances favor, for instance, the existence of metastable atomic states and the transport of excitation energy or the occurrence of self-multiplicating chain phenomena, a phenomenon starting from a single atom may spread over distances of even microscopical order. Therefore, the argument outlined by Delbruck (1940) that the linear dimensions of the "effective volume" for the production of gene mutations ($\approx 1 \mu\mu$) are already so large that the sensitive region cannot reasonably be still much larger, might not be very conclusive.

Arbitrary neglect of the physical factor (i.e. assuming $p = 1$) leads to the acceptance as a correct estimate of the size of the sensitive region of what actually is its minimum value. In fact, the physical factor reduces the average efficiency of radiation. The more important is the physical factor (i.e. the smaller is p), the larger is the ratio of the size of the sensitive region to the measured "effective volume" τ .

In conclusion, the broadest interpretation of the hit theory based on the assumptions (a), (b), and (c) given above leads to the definition of an effective volume τ which is a probability. (The "effective volume" as used here corresponds to the "sensitive volume" as used by Muller, 1940, and to the "action volume" as used by Wollman *et al.*, 1940, while Muller's "potential sensitive volume" corresponds to the volume V of the sensitive region.) Although this probability certainly involves a factor related to the size of a sensitive region, there is not much evidence to assume further that this is the only important factor, so that one might identify the "effective volume" τ with the size of a target or sensitive volume.

3. The problem of the "nature of the hit"

Attempts have been made to identify the "hit" with some one of the physical phenomena produced by radiation within matter. The most usual method which has been applied mainly to the X-ray production of gene mutations (e.g. Timofeeff-Ressovski, 1937) will be outlined first. Three possible cases are considered, namely that the "hit" consists of:

(a) Absorption or scattering of an X-ray quantum, and consequent production of a secondary electron, within a target.

(b) Passage of a "secondary electron" across a target.

(c) Production of an ionization by a secondary electron within a target.

Neglecting the physical probability factor, the size of the target is equal to the constant k in formula (1). The proper choice of the unit of the X-ray dosage is: in case (a), the production of one secondary electron per cc. of matter; in case (b), the flow of one secondary electron per sq. cm. within matter; in case (c), the production of one ionization per cc. of matter; this last unit is essentially a submultiple of the roentgen unit. The ratios among these three units, and hence the ratios among the corresponding evaluations of the target, can be determined with good approximation on the basis of physical data and depend on the wave-length of the X-rays. Experiments with different wave-lengths, where no saturation effect is observed, show that the size of the target is independent of the wave-length in case (c) but variable in the cases (a) and (b). Since the target cannot actually vary, only (c) is acceptable.

This procedure is a device by which to select one from among different working models. Successful comparison with experiments may, however, lead the working model (c) to be considered as wholly successful, even though only a part of its features is involved in the comparison. It will be shown that the results of the experiments with X-rays of different wave-lengths do not actually support the model representing a "hit" as an ionization within a target, but they can be interpreted *independently of the hit theory*.

The quantity k in the formula (1) is essentially a measure of the efficiency of a unit of radiation. An experimental result which is interpreted by the hit theory as a variation of the size of the target actually means a variation of efficiency, since it

shows that an equal number of radiation units produces different biological effects in different cases. Thus the experiments on the production of gene mutations with X-rays of different wave-lengths show that the efficiency of each ionization produced by X-rays is constant. The *distribution* of the ionizations is *immaterial* and the biological action depends only on the *total number* of ions produced by all the secondary electrons.

One may then conclude that (within the limits of these experiments) the physical action of a secondary electron is not biologically effective as a whole. Different ionizations produced by the same or by different electrons do not participate as a cooperative team to the biological action, but their actions are merely superimposed. Each ionization is somehow biologically effective by itself and may be considered as *an independent cause* of the biological action. This does not necessarily mean that a single ionization is sufficient to produce an appreciable biological change, but that it is able to contribute somehow by itself to this action without any need for immediate cooperation by other phenomena, or else, that it may suitably be considered as a "unit of action." This is an extract of the concept of "hit" excluding those elements of this concept, which correspond only to working models.

Thus, although secondary electrons are themselves in a way the cause of mutation, their action can be analyzed showing that single subunits of its physical action (the ionizations) may be considered as a *nearer cause* of the biological action. The procedure which is usually intended to determine the "nature of the hit" may be considered as an analysis of the secondary physical action of radiation aiming at identifying the nearest cause of its biological action. A pattern of analysis along this line, following step by step the chain of secondary phenomena, is shown below in Section 5.

It is not quite correct to focus attention only on ionization phenomena. Atomic excitation phenomena should also be considered, in which energy is delivered to a single atom without removing any one of its electrons. Furthermore, one must distinguish between the atomic phenomena produced directly by photo- or Compton-electrons and the phenomena produced indirectly through the action of the tertiary electrons ejected whenever an ionization occurs. The total number of ionizations is, however, a fair index of the whole of the atomic

phenomena produced by radiation, since the relative frequency of different phenomena and the mean amount of energy distributed to matter "per ionization" are widely independent of the quality of radiation. Further details on this subject will be given in Section 5.

4. The saturation effect

Biological actions do not always depend only on the number of ionizations produced by radiation, as the production of mutation by X-rays does, but they sometimes depend also on the density along the tracks of ionizing particles. Cases are known in which the biological effectiveness of ionizations increases when the ion density along the tracks of the ionizing particles is increased and cases are also known in which the effectiveness decreases under the same conditions. The first phenomenon has been sometimes called "concentration effect"; it clearly must occur when single ionizations are not very effective but their effectiveness is improved by the cooperative action which is possible at high concentration.

The opposite saturation effect, i.e. a loss of effectiveness at increasing concentration of ions, has already been discussed from the standpoint of the hit theory in Section 1, but will be further analyzed here, independently of the hit theory. The average biological effectiveness of a flow of ionizing particles is represented by the constant k of formula (1) when the dose is measured as a flow of particles per unit area within matter; k is then an "effective cross section," (see Section 2). The ion density along the track of the particles is simply a measure of the energy absorbed by matter (see above and Section 5). When the ion density is small and there is no saturation effect, as in the X-ray production of mutations, the effectiveness of the flow of particles is proportional to the energy delivered to matter per unit path. This is a quite understandable result without any reference to the hit theory. As the ion density increases, however, the effectiveness cannot be expected to remain proportional to the energy absorption so as to increase beyond any limit, because particles passing too far away from the genetic material are not expected ever to be effective, no matter how concentrated their physical action may be. At best, if the ion density were so large that the action of ionizing particles is smashing and decisive, all those, but only those, particles passing close enough to the genetic material would be effective. (The

"effect" means here the occurrence of one among all the possible alternative changes, as, e.g. the mutation of a gene to one among all its alleles.) The extreme case of particles which are effective whenever smashing across some sensitive region does not seem to have yet been observed but would afford a concrete application of the concept of "hit." In this case the effectiveness of ionizing particles would be fully "saturated" and would not increase any further with increasing ion density: its constant value would yield a direct measurement of the average cross section of the sensitive region. These considerations assume merely that the concept of a sensitive region is correct to some extent.

The "effective volume" τ defined in Section 2 is the ratio of the effectiveness of ionizing particles to the ion density along their paths. Thus τ is constant as long as the effectiveness is proportional to the ion density (no saturation). At full saturation, on the contrary, the effectiveness is constant and τ is proportional to the ion density.

In any practical case the effectiveness of ionizing particles is not known to have reached its maximum value and it yields only a minimum estimate of the size of the sensitive region. Such estimate is carried out here as an example, accurate within an order of magnitude, for the production of sex-linked lethals in *Drosophila melanogaster*. The "effective volume" τ is of the order of 10^{-17} cm.³, both for X-rays and neutrons. In the neutron experiments the recoil protons induce approximately 10^7 ionizations per cm. path; hence the flow of one recoil proton per cm.² corresponds to 10^7 ionizations per cm.³ Accordingly, the value of k which can be called "effective cross section" must be 10^7 times larger than τ :

$$10^7 \times 10^{-17} = 10^{-10} \text{ cm.}^2$$

The next objective is to investigate the relationship between the effectiveness and the ion density when the ion density is neither very low nor very large. Its qualitative behavior is indicated by the broken line in Fig. 1. The two short segments at the beginning and at the end of this curve, which are indicated by a solid line, represent the results stated above, namely: (a) the effectiveness is expected to be proportional to the energy absorption when the energy absorption is very small, and (b) the effectiveness should not exceed a maximum limit which is determined by

the size of a sensitive region and which might be attained only at very high ion density. If it were possible to represent the whole curve by a theoretical formula involving a number of unknown parameters, one could determine the value of the parameters by fitting a sufficient number of experimental points and thus determine the maximum effectiveness and hence the size of the sensitive region.

If all the individual particles which cross the sensitive region delivered the same amount of energy within it and if all parts of the sensitive region were equally sensitive, one might expect the saturation effect to step in sharply at a certain ion density, as indicated by the dotted line in the figure. If, on the contrary, the energy delivered by different particles, or the local sensitivity, is variable, saturation must step in gradually: At any given value of the mean ion density the physical action of some particles which by chance deliver more energy, or which deliver it at more effective points, may already be excessively crowded and thus, on the average, less effective, while the effectiveness of other particles is not yet reduced, being still sufficiently small. One may imagine that the particles are classified into many different groups with homogeneous effectiveness, each of which is affected by saturation abruptly—as indicated by the dotted line in Fig. 1—but at a different value of the mean ion density. The final relationship between the average effectiveness of all particles and the mean ion density is then represented by an average of dotted lines with variable scale of abscissae. The larger is the variability, the more will the final (broken) curve depart from the shape of the dotted line.

There are several factors of variability. First, the lengths of the paths of the ionizing particles across the sensitive region cannot be all equal, depending on whether the crossing is central or not. This factor is variously important according to the shape of the sensitive region; it is least important in the case of a spherical shape (this shape is most compact because its surface is a minimum for a given volume). Second, there are fluctuations of the energy actually delivered by ionizing particles within paths of equal length. This again is due to various causes: (a) An ionizing particle undergoes discontinuous energy losses producing ionizations and excitations distributed at random along its track; the number of energy losses within the path across the sensitive region may vary strongly unless

this path is much longer than the average distance between successive energy losses (the hit theory has been mainly concerned with this factor). (b) The amount of energy lost in any single process is also highly variable. (c) Beside the random variations considered under (a) and (b), the amount of energy lost and the ion density undergo a systematic increase along the path of an ionizing particle which is progressively slowed down; moreover, even the initial velocity of the particles is not uniform, when they originate as Compton-electrons or recoil protons. Third, there may be variability of sensitivity in different parts of the sensitive region; this variability might even make the concept itself of a sensitive region hardly significant, if it is very smoothly graded.

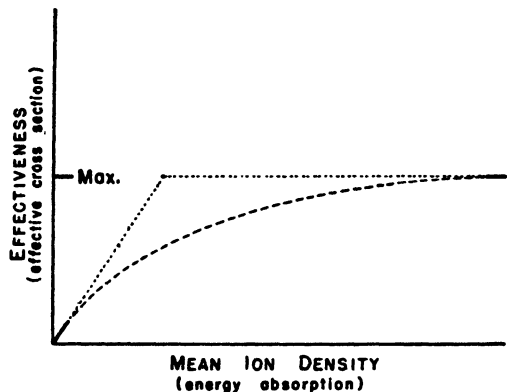


FIG. 1. GRAPHICAL REPRESENTATION OF THE SATURATION EFFECT
(See discussion in the text)

The theory developed by Lea (1940) takes into account only that part of the variability factors which is most easily accessible to quantitative investigation, namely: (a) the variability of the length of the path across the sensitive region and this only for the extreme case of a spherical shape, (b) the variability of the number of energy losses within any given length of path, without any reference to the amount of energy. Neglect of the other variability factors makes Lea's curve depart too little from the shape of the dotted line in Fig. 1. Hence any evaluation of the upper limit of the effectiveness, that is, of the size of the sensitive region, which is based on fitting Lea's curve to experimental results is bound to give a result which is *certainly smaller* than the correct one. The assumptions made by Lea do not correspond to the choice of an average but of an extreme case. The

quantitative accuracy of Lea's curve has not yet been evaluated.

Lea's neglect of the "physical probability factor" does not affect the shape of his curve: The course of saturation is the same, whether, for example, an ionization has the probability 1 or only 1/10 of producing a mutation; in the last case, however, the ion density must be ten times larger to produce the same saturation effect.

According to Lea's theory, the knowledge of the "effective volume" τ for a single value of the ion density is sufficient to determine its value at any other density. Qualitatively: Calling V the volume of the sensitive region, τ must be equal to V at low ion density and then become smaller when the average distance between successive ionizations is $\approx \sqrt[3]{V}$.

In more complex cases, two independent quantities must be determined separately. For instance, in the case of the sex-linked lethals Lea considers the unknown "number of genes" n which measures the departure from the spherical shape when the target consists of separate parts: Then $\tau = nV$ at low ion density; this, together with an independent determination of the critical ion density $\sim 1/\sqrt[3]{V}$ at which saturation becomes apparent, enables Lea to determine both V and n . Another example: The "physical factor" introduces the unknown probability p ; then $\tau = pV$ at low ion density, while the critical ion density is $\approx 1/\sqrt[3]{V}$.

When, however, the departure from the spherical shape and the "physical factor" and, furthermore, the other variability factors listed above are all considered at the same time, the dependence of τ on the ion density becomes so complex that the quantities like V and p cannot be easily determined.

Thus there does not seem to be much conclusive evidence supporting Lea's detailed interpretation of the saturation effect on sex-linked lethals in *Drosophila*. It is possible, however, to apply the saturation effect to test whether the sex-linked lethals consist of alternate independent mutations at different loci and whether each one of these mutations is analogous to the individual phenotypically detected mutations. If it is so, the saturation effect should affect equally the production of all the lethals and of the individual phenotypical mutations. Then the ratio of the frequency of all sex-linked lethals to the average frequency of individual mutations should be approximately independent of the ion density and represent approxi-

mately the number of possible different lethals in the X-chromosome.

5. Investigation of the "nearest cause" of a biological action and remarks on the physical action of X-rays

As a first step of analysis it must be checked whether single X-ray quanta can be considered as an "independent cause" of any biological effect under consideration, for example of mutations, in the sense considered in Section 3. This can be done by testing experimentally that the distribution in time of the radiation quanta has no bearing on their effect.

Secondary electrons must be considered in a successive step. Soft X-ray quanta interact primarily with matter only through the production of a single photo-electron, whereby they disappear; thus the action of a quantum can be identified with that of a photo-electron. Hard X-ray quanta produce many secondary Compton-electrons through successive scattering processes; these processes occur, however, on the average, so far apart as compared to cytological dimensions, that immediate cooperation between "brother" Compton-electrons can be disregarded. Hence in any case individual secondary fast electrons can be considered as "independent cause" of the biological effect.

Fast electrons, as well as all other fast charged particles, traversing matter undergo a large number of energy losses in which a small fraction of their kinetic energy is transferred to individual electrons within matter. These energy transfers from fast electrons, henceforth called "energy transfers," are governed by important rather simple laws. The amount of energy transferred in a single energy transfer is highly variable and averages ≈ 30 electron-volts. Small energy transfers are much more frequent than large ones. If the energy transfer exceeds a limit characteristic of the kind of matter, of the order of ten electron-volts, the electron absorbing this energy can abandon the atom or molecule to which it was previously bound (ionization). If the energy transfer is smaller, a simple electronic excitation occurs. *The relative frequency of the various kinds of energy transfers is approximately independent of the energy of the impinging electron* (and depends very little on whether the impinging particle is an electron or an heavy particle, provided that they have the same charge and velocity). The total frequency of energy transfers

along the path of a fast electron, on the contrary, is *approximately inversely proportional to the energy of the electron*. Therefore, a change of the wavelength of the X-rays, which means a change of the energy of the quanta and hence a change of the energy of the secondary electrons, does not affect appreciably the quality of the energy transfers but only their density along the electron tracks. The total amount of energy loss and the number of ionizations produced are proportional to the number of energy transfers; thus the measurements of X-ray dosages in roentgen units may also be expressed as a "number of energy transfers per unit volume." The frequency of production of gene mutations by X-rays is then proportional to the number of energy transfers independently of their density along the tracks of secondary electrons. Therefore, single energy transfers can be considered as independent units of action, or as "a nearer cause of gene mutations."

As mentioned in Section 4, energy transfers are not always independent units of action when they occur too close to each other. This might happen because the effect of one energy transfer excludes, or makes useless, an analogous effect of other energy transfers, as in the saturation effect, or, on the contrary, because cooperative action of two adjacent energy transfers is helpful to produce an effect. A still different interaction due to quantum mechanical interference phenomena may occur when more than one energy transfer takes place within a single molecule.

Consider now the phenomena associated with an energy transfer. On the average, approximately one out of three energy transfers produces an ionization, i.e. ejects an electron from its place; the other energy transfers produce simple excitations. An excess positive charge is temporarily left in the atom or molecule (positive ion) from which an electron has been removed. The ejected (tertiary) electron undergoes a series of processes analogous to the energy transfers. These processes often occur very close to each other because of the small energy of the tertiaries. When the energy of an electron is so small that it cannot excite any more atoms, the electron keeps on wandering and undergoing large deflections until it is captured somewhere with release of excitation energy; most frequently it is captured by a neutral atom with formation of a negative ion. Positive and negative ions tend finally to neutralize their charges with further release of energy. A large

fraction of the tertiary electrons have not sufficient energy to produce any ionization; very few of them produce very many ionizations. On the average, two ionizations arise, directly or indirectly, from every tertiary electron. Thus the ionizations produced by tertiaries bear to those produced directly by secondaries the same ratio (2:1) as the energy transfers without ionization bear to those with ionization; hence the total number of ionizations is just about equal to the number of energy transfers of secondary electrons.

No method is available to vary the spatial distribution of the ionizations and excitations accompanying an energy transfer, because, as stated above, the quality of the energy transfers does not depend appreciably on the quality of radiation. Therefore it is impossible at present to analyze the "cause" of the production of gene mutations beyond the stage of the physical action represented by the energy transfers of the secondary electrons. *Therefore it is also impossible to recognize single ionizations as independent units of action:* Some previous interpretations have been inexact on this subject, inasmuch as it was not considered that a change in the wave-length of X-rays does not affect the distributions of ionizations along the side-tracks of tertiary electrons, but only the distribution of energy transfers of secondary electrons. Also, in the previous sections of this paper "energy transfers" should always be considered instead of ionizations.

Jordan (1938b) and Lea (1940) recognized the impossibility of analyzing the action of the energy transfers and considered the production of a tertiary electron together with its whole action as the fundamental unit of action, the "ion cluster." An ion cluster contains on the average three ionizations (see above) but this average value is not the most frequent one (single ionizations are most frequent). Considering ion clusters as the fundamental units means neglecting all those energy transfers which lead to simple excitations.

A few more remarks can be made concerning the biological importance of ionization phenomena. On the one hand, the separation of charges which takes place at ionization gives rise to a metastable storage of activation energy which is released only at recombination; the longer this energy is available, the more likely it is that it can be used for any specific purpose, as, for example, for a biochemical change. Moreover, the separated charges might conceivably affect electrostatically

the physico-chemical phenomena involved in biological systems. On the other hand, however, the amount of ionization produced by radiation is an important quantity mainly because it is directly measurable, at least in gases, and because it represents a fair index of the amount of energy absorbed by matter and of the number of energy transfers of fast secondary electrons. The single ionizations themselves should not be considered as the units of biophysical action on the basis of the present knowledge, as shown above. Biochemical reactions may be activated by radiation independently of any ionization, that is, by simple excitations.

The distribution in space of negative ions is the result of a long process of diffusion of very slow electrons and has little bearing on biological actions. Therefore it is important to distinguish between the distributions of ions of different sign. Cloud chamber pictures may give a misleading picture of the spatial distribution of radiation effects, inasmuch as they do not show this distinction. Finally the difference between the distributions of positive and negative ions has been disregarded in theoretical calculations of the ion recombination, which were directed to determine the radius of action of α -particles (Jaffe, 1914; see also Jordan, 1938a). Therefore values too large have been obtained for this quantity.

SUMMARY

The interpretation of radiogenetic experiments, which is given by the hit theory, may be subjected to criticism. The random distribution in space of the physical action of radiation seems to be only one among the factors determining the frequency of mutations. The lack of influence of the wave-length of X-rays on their genetic effects can be discussed and understood independently of the hit theory. A generalized treatment of the dependence of the effectiveness of radiation on the ion density enables us to consider the influence of several hitherto neglected factors on the theoretical relationship calculated by Lea (1940). A modified pattern of biophysical analysis of the X-ray action is suggested, showing that the procedure usually intended to determine the "nature of the hit" is

equivalent to an investigation of the "nearest cause" of a radiobiological action.

LIST OF LITERATURE

- DELBRUCK, M. 1940. Radiation and hereditary mechanisms. *Amer. Nat.*, 74, 350-362.
- FANO, U. 1941. An analysis of chromosomal changes in *Drosophila*. Cold Spring Harbor Symposia IX.
- FRICKE, H., and DEMEREC, M. 1937. The influence of wave-length on the genetic effects of X-rays. *Proc. Nat. Acad.*, 23, 320-327.
- GRAY, L. H., and READ, J. 1939. Measurement of neutron dose in biological experiments. *Nature*, 144, 439-440.
- JAFFE, G. 1913. Zur Theorie der Ionisation in Kolonnen. *Ann. der Physik.*, 42, 303-344.
- JORDAN, P. 1938a. Ueber die Elementarprozesse der biologischen Strahlenwirkung. *Radiologica*, 2, 16-35.
- . 1938b. Biologische Strahlenwirkung und Physik der Gene. *Physik. Zeits.*, 39, 345-366.
- . 1939. Zur Quanten-Biologie. *Biol. Zentralblatt*, 59, 1-39.
- LEA, D. E. 1940. A radiation method for determining the number of genes in the X-chromosome of *Drosophila*. *J. of Genetics*, 39, 181-188.
- MULLER, H. J. 1940. An analysis of the process of structural change in chromosomes of *Drosophila*. *J. of Genetics*, 40, 1-66.
- TIMOFEEFF-RESSOVSKI, N. W. 1937. Mutationsforschung in der Vererbungslehre. 1-181. *Dresden and Leipzig*.
- WILHELMY, E., ZIMMER, K. G., and TIMOFEEFF-RESSOVSKI, N. W. 1936. Versuche mit sehr weichen Roentgenstrahlen an *Drosophila melanogaster*. *Strahlenther.* 57.
- WOLLMAN, E., HOLWECK, F., and LURIA, S. 1940. Effect of radiations on bacteriophage C₁₄. *Nature*, 145, 935-936.
- WYCKOFF, R. W. G. 1930a. The killing of certain bacteria by X-rays. *Jour. Exp. Med.*, 52, 435-446.
- . 1930b. The killing of colon bacilli by X-rays of different wave-lengths. *Jour. Exp. Med.*, 52, 769-780.
- ZIMMER, K. G. 1938. Dosimetrische und Strahlenbiologische Untersuchungen mit schnellen Neutronen I. *Strahlenther.*, 63, 519-527.
- , and TIMOFEEFF-RESSOVSKI, N. W. 1938. Dosimetrische und strahlenbiologische Untersuchungen mit schnellen Neutronen II. *Strahlenther.*, 63, 528-536.



NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of THE QUARTERLY REVIEW OF BIOLOGY, Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore, Maryland, U. S. A.

INCREASE AND MULTIPLY

Being a review of *Nation and Family* by Alva Myrdal, New York (Harper and Brothers), 1941. Pp. xv + 441. 9½ x 6 inches. \$4.00. By Antonio Ciocco, U. S. Public Health Service.

Man, long ago, made the interesting discovery that there are means whereby the mating urge could be satisfied while the chances of reproduction are materially reduced. This discovery has been one of the main elements to upset the best laid plans of social reformers who seek to regulate the sexual activities of the individual. The tremendous technological progress of the last century and the great increase in scientific knowledge have extended also to the field of contraception and birth-prevention, and as a consequence those who guide the destinies of the societal group as well as its morals are faced with an increasingly baffling problem. Their difficulties are enhanced at present because contemporary students of population have reversed the viewpoint of the preceding generation and clamor about the dangers of depopulation. During the past two decades in Belgium, France, Germany and Italy, legislative measures to stimulate child-bearing have been introduced. Sweden has followed suit and between 1934 and 1938 a Population Commission within the Swedish legislative body was organized to study the "population problem." In this book Myrdal summarizes the work of the Commission and comments on the results achieved, the recommendations made, and laws passed.

Sweden has a population of only about 6½ millions and it is predominantly a non-industrial country, yet it has always claimed the interest of demographers and other social scientists. The reasons are rather obvious. First, the present system of vital statistics registration dates back a long time and is one of the most reliable of any country. Second, the Swedes have experimented with many social reforms on a national scale without abandoning any of the overt characteristics of a democratic form of government. This has led many to see

in Sweden the paragon of our civilization and to advocate imitation of its mores and laws. Even if this were possible, there are many features of the demographic trends in Sweden that deserve careful consideration. They are clearly outlined in the first part of the book, in the excellent description of the population characteristics of the country. The population has been increasing very slowly; the death rate has declined to a level below which it cannot go; the marriage rate is low; and the illegitimate birthrate is high. Thus, as many students of population prophesied, the trends of mating behavior seem to lead to a breakdown of the family as at present constituted. The author fears it and so apparently have the Solons of Sweden.

To forestall the danger, the Swedish Population Commission suggested a number of measures certain of which have been enacted into laws. The measures proposed and instituted, described in the second part of the book, not only serve to relieve from all of the classes of the population some of the economic burdens which accompany the formation and maintenance of a household, but go much further in the direction of repealing what are still considered, in this country at least, fundamental principles of morality. Anti-contraceptive laws are abolished, and sex education is regarded as an item of the scholastic curriculum. Laws regarding sterilization and the induction of abortions have been broadened but to what extent is not clear from the author's exegesis. As Myrdal points out the enactment of these laws constitute a victory for the neo-Malthusian movement. They certainly represent a frank recognition of the sex problems but in what manner they will stimulate the production of babies is not easily understood. However, there are other measures that bear directly on the matter of encouraging childbearing. Within the framework of sickness insurance and free medical care—measures which place Sweden in the vanguard relative to State medicine—the government furnishes loans to married couples preparing to set up a household; gives a "maternity bonus" to all mothers, except those in the

high income brackets; provides for free school lunches for children; provides for equality of treatment of married and unmarried mothers, legitimate and illegitimate children. How successfully will these measures achieve their purpose? The author is hopeful but also points out that the laws still assume that the woman is to be fundamentally a home-maker, a function which she shows little desire to exercise so long as she has economic opportunities equal to those of the male. It is likely that the author has perceived and indicated the crux of the contemporary problem. If this is so, one can expect that the Swedish experiment will give results similar to those achieved in other countries and in other periods. The failures of the past derive not from lack of sizeable

efforts but from the naïveté of the reformers who see the "problem of population" now as a problem of economics alone, now as one of moral behavior only and so on, but never in its entirety, as a problem of human biology. Although the author does take a broader view than usual of the problem, one notes unnecessary emphasis on the (a) need for and value of positive action, (b) goodness of the measures adopted in Sweden, and (c) distinction between the Swedish laws and those of other countries. Nevertheless, it can be said that this work constitutes one of the most interesting surveys of the population problem within the past decade, and one which will undoubtedly influence greatly American thought on the subject.

BRIEF NOTICES

EVOLUTION

PROBOSCIDEA. *A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World. Volume II. Stegodontoidea, Elephantoida.*

By Henry Fairfield Osborn. Edited by Mabel Rice Percy. The American Museum Press, New York. \$20.00. 12½ x 10½; 805-1675 + 30 plates + 2 folding charts; 1942.

Somebody once told a story of an international competition for the best book on elephants. It supposedly produced manuscripts by an Englishman on "Where and how to shoot elephants," by a Frenchman on "L'elephant et ses amours," by a German for a "Handbuch des anatomischen Aufbaus und der geographischen Verbreitung der vorgeschichtlichen Elefanten und ihrer jetztzeitlichen Verwandten, mit einem Anhang über die Entwicklungsgeschichte des Zähnsystemes," and by an American, who won the prize, on "The American Imperial Elephant, the biggest of them all." To some laymen it may also be merely amusing to hear that someone has actually written nearly 2500 large printed pages on the history of a group of mammals of which our recent elephants are the last survivals. If, however, they will examine this monumental and admirably illustrated work, they will find that this is the best documented, most nearly complete and, hence, the most convincing account of the entire evolution of one animal group that it has ever been possible to assemble. This scholarly history of the order of proboscideans by America's foremost palaeontologist, the late Professor Osborn, covers a period of some 60,000,000 years, spreads over four continents and reveals nature's constantly changing and widely diverging experiments in producing the largest of all terrestrial mammals.

The first volume of this monograph appeared in 1936 (reviewed in this Journal, vol. 12, p. 211), the year after its author's death. The present, second volume has been very ably edited by Osborn's former secretary,

Miss Mable Percy. There has been added a chapter on the geologic succession of the proboscideans by one of Osborn's former assistants, E. Colbert, and a brief appendix on proboscidean dental histology by G. G. Simpson. The second volume deals with the last two of the five proboscidean suborders or superfamilies, the Stegodontoidea and the Elephantoida and contains the general summary regarding the affinities, migrations, and phylogeny of the entire order. Here are also given a supplementary bibliography and the general index for both volumes.

The enormous amount and varieties of fossil remains which form the basis for the large descriptive parts of this work have been unearthed over a period of more than three hundred years. In this material Osborn distinguished 5 superfamilies, 8 families, 21 subfamilies, 44 genera, and 352 valid species and subspecies. No wonder the pedigree of the Proboscidea is a vastly complex affair; and still there remain undoubtedly many gaps in our knowledge of ancestral elephants to be filled by future discoveries! The construction of this pedigree is based to a large extent upon the careful analysis of the remarkable and manifold specializations in the dentition. It has been possible to show that all the many forms of molars are derived from simple four-crowned ancestral grinding teeth. Numerous evolutionary trends, accounting for the varied changes in the skeleton are demonstrated step by step with a wealth of technical detail which itself had facilitated the conscientious reconstructions of the outer forms of the amazing array of extinct proboscideans.

Osborn has been equally interested in the evolution of man as in that of the elephant. Comparisons between these two great histories often occupied his mind, as is indicated by the following paragraph from his own pen, quoted in the summary of the volume under review:

An insatiable *Wanderlust* has always possessed the souls of elephants as it has those of the tribes and races

of man. Not only to overcome the changes and chances of this mortal life, but also to gratify their intelligent curiosity ever to explore afresh forests, pastures, fields, rivers, and streams, they have gone to the very ends of the earth and have far surpassed man in adapting their clothing and teeth to all possible conditions of life. Thus the romances of elephant migration and conquest are second only to the romances of human migration and conquest. Variety is the spice of elephant life, as it is of human life, and the very longing for a change of scene and of diet has been the indirect cause of what in scientific parlance we term *adaptive radiation*—the reaching out in every direction for every kind of habitat, in itself the cause of radiating or divergent evolution and adaptation. It is to this predisposition to local, continental or insular, and world-wide wanderings that we attribute the many branches and sub-branches which have been developed in this remarkable family.



A MIDDLE EOCENE FLORA FROM THE CENTRAL SIERRA NEVADA. *Contributions to Paleontology, Carnegie Institution of Washington Publication 534.*

By Harry D. MacGinitie. *Carnegie Institution of Washington, Washington, D. C.* \$2.50 (cloth); \$2.00 (paper). 11½ x 8½; iii + 178 + 47 plates; 1941.

It was the search for gold back in the era of the "forty-niners" that the outcrop of plant-bearing sediments were first uncovered in the Sierras. MacGinitie gives a brief account of the development of gold mining from placer methods to hydraulic mining, and the manner in which the beds became known.

The miners became, indirectly, fossil collectors, since they piled the silicified logs . . . which occur in abundance, in windrows along the edges of the sluicing channels in order to facilitate the movement of the finer gravel. They also noted the fossil leaf impressions in the clay beds. These were brought to the attention of the United States geologists under J. D. Whitney about 1875. A good collection was made at Chalk Bluffs and sent to Leo Lesquereux for determination. . . . Lesquereux . . . published the results of his study as a *Report on the fossil plants of the Auriferous Gravel deposits of the Sierra Nevada*. This report is one of the classic papers in the literature of paleobotany.

The present work is concerned with the fossil plants of Chalk Bluffs, a region 50–60 miles northeast of Sacramento, with an elevation varying from 1000 to 3000 feet. The various localities from which the Chalk Bluffs flora came are all considered to fall in the same stratigraphic horizon, with the possible exception of that at Cherokee. Fossil collections were first made about 1870 but the localities were temporarily lost after the decline of gold mining in the region. It was not until 1931 that members of the U. S. Forest Service rediscovered the rich fossil deposits.

MacGinitie began his survey in 1933. In the present paper he gives interesting discussions of the geology of the region, climate and vegetation, composition of the flora and relationships of the fossil species, and

environment of the fossil flora (including geographical distribution of similar living species, abundance of fossil species, ecological and climatic conditions, distribution and related problems). He finds that "The Chalk Bluffs flora is shown by its composition and state of evolution to be the oldest of the six well known older Tertiary floras of the Pacific slope." The forms represented (over 75 are described) indicate a humid, sub-tropical climate for this region in early geologic times. Existing representations of these forms inhabit two areas: Southeastern North America including Mexico and Central America, and Southeastern Asia. Of the fossil angiosperm species, 36, or 54 per cent, are trees; 24, or 36 per cent, are shrubs or small trees; and 7, or 10 per cent, are vines.

The excellent illustrations show characteristic views of the Chalk Bluffs region, modern forest vegetation of California and Mexico (9 plates), and fossil types (38 plates). A useful bibliography of four pages is included and an index of genera and species.



HOW MAN BECAME A GIANT.

By M. Ilin and E. Segal. Translated by Beatrice Kinhead. Illustrated by A. Komarov and E. A. Furman. J. B. Lippincott, Philadelphia. \$2.00. 8 x 5½; 270; 1942.

"There's a giant in the world. He has hands that can lift a locomotive without the least effort. He has feet that can travel thousands of miles in a single day. He has wings that can carry him up above the clouds, higher than a bird can fly. . . . He has eyes that can see the invisible. . . . This giant is man." In this fashion the meaning of the title is explained in the introduction of this book for adolescents on man's rise above his animal ancestry.

This is a vivid popular account of human evolution with the main emphasis on the development of man's ability to fashion tools, to build homes, to formulate language and social organization, etc. In general, the authors have been guided closely by the best scientific evidence, so far available, but at times they draw rather heavily upon their imagination, particularly in those parts of the story regarding which the scholar would still have to admit large gaps in his knowledge.

Among the many recent attempts to reconstruct man's remote history for the layman, this little volume recommends itself by notable originality, good style and very attractive illustrations. Throughout, the one theme is developed enthusiastically and convincingly: Man was once the slave of nature, as are all his fellow creatures, but he freed himself and became the master of the world. It is not even mentioned, however, that man has progressed pitifully little toward mastering his own nature.

GENETICS

THE GENETIC AND ENDOCRINIC BASIS FOR DIFFERENCES IN FORM AND BEHAVIOR as Elucidated by Studies of Contrasted Pure-Line Dog Breeds and Their Hybrids. *American Anatomical Memoirs*, Number 19.

By Charles R. Stockard and Collaborators with Special Contributions on Behavior by O. D. Anderson and W. T. James. The Wistar Institute of Anatomy and Biology, Philadelphia. \$7.50. 10 x 6½; xx + 775 + 113 plates; 1941.

The demonstration that, in human beings, extreme diversities in type and constitution are associated with various modifications and diseases of the endocrine glands has led a number of investigators to suggest the possibility that hereditary modifications of the glands of internal secretion may account for the establishment of racial differences in man. It can be imagined that some relatively simple change in the genetic constitution which would bring about over-activity or under-activity of one or another of the endocrine glands might result in the establishment of a type which would be very distinctive both in its form and behavior. In such a case, the endocrine complex would become an important intermediary mechanism in evolution. The attempts of the late Doctor Stockard to test this thesis by exhaustive investigations of the morphological and behavioral characteristics of various pure breeds of dogs and their hybrids mark a milestone in the development of the study of endocrinology.

The data presented in the present monograph give in detail the results of the work at the Cornell Anatomy Farm since 1926. It is indeed fortunate that the greater part of the manuscript had been completed by Stockard before his death in 1938 but it is a matter of great regret that certain sections, notably the final integration of the results concerning the relation of the endocrines to type, are lacking. Without such an integration the various sections of the book stand as more or less isolated contributions, and to arrive at a general picture of the results of the work as a whole is somewhat difficult. It is clear that despite the great mass of material which has been obtained and the critical care with which it has been weighed and presented, many phases of the work are still in preliminary stages. Knowledge of the genetics of the various breeds of dogs is still relatively limited and the constant association of particular histological characteristics of the endocrine glands with particular physical types of dogs is by no means proved. These difficulties were clearly recognized by Stockard, however, and the data are presented with the reservations which these limitations demand. This is a pioneering investigation carried out with patience, insight and care, and its results are of great significance not only in relation to the immediate problem at hand but also to many other lines of work.

GENERAL BIOLOGY

BIOLOGICAL SYMPOSIA. Volume IV. I. *Population Problems in Protozoa*. II. *Experimental Control of Development and Differentiation*. III. *Theoretical and Practical Aspects of Polyploidy in Crop Plants*. IV. *The Species Problem*.

Edited by Jaques Cattell. Foreword by Sewell Wright. The Jaques Cattell Press, Lancaster, Pennsylvania. \$2.50. 9½ x 6½; xi + 293; 1941.

This book includes four symposia on such diverse subjects as Population problems in Protozoa, Theoretical and practical aspects of polyploidy in crop plants, Experimental control of development and differentiation, and The species concept.

The first symposium is concerned primarily, though not exclusively, with laboratory populations. Effects of both the composition of the environment and of interactions between organisms are considered. There is first a brief historical introduction followed by papers on the ecological aspects of natural populations, on laboratory populations of flagellates, of ciliates, of blood-dwelling forms, and finally a paper inter-relating the work on protozoan populations to work on populations of animals in general. Particular emphasis is laid on the effect of the density of the original population on growth.

The second symposium deals with several aspects of polyploidy. The practical aspects of the subject are dealt with in papers giving the results of induced polyploidy in floriculture and in breeding of crop plants. The method seems to be of value both in the immediate production of new varieties and in the transference of genes from one variety or species to another. The use of polyploidy in investigating more theoretical matters is shown in two other papers; one giving the results of investigations on evolution in the genus *Nicotiana*, the other discussing the occurrence and distribution of mutations in polyploids.

In the third symposium, four papers are given on particularly well analyzed developmental systems. The first discusses the systems of reactions leading to eye pigmentation in *Drosophila* with emphasis on the rôle of individual genes. The second considers the effects of induced polyploidy on development in plants, particularly *Datura*. The third treats the developmental reactions leading to the production of feather color patterns in the domestic fowl. Particular emphasis is laid on studies of the interaction of melanophores and feather germs of different breeds. The final paper deals with investigations of the rôle of hormones in plant development.

The last symposium is concerned with an analysis of the species concept and with some of the factors involved in species formation. The first paper is primarily a discussion of the species as viewed by the museum taxonomist. The method of action of natural selection

is considered in the second paper with emphasis placed on selection of physiological characters with incidental selection of correlated morphological characters. The third paper discusses geographical varieties in certain plants with an evaluation of the rôle of heredity and environment in determining the characteristics of the individual plant. The last paper is a consideration of the rôle of isolation on speciation in the insects of the Hawaiian islands. The symposium emphasizes the information on evolution that may be derived from morphological and taxonomic studies in the field.

In general this series of symposia is an excellent addition to the previous ones. The value of most of the papers is enhanced by short lists of references, though in a few cases such lists are regrettably lacking.



GENERAL BIOLOGY FOR COLLEGES.

By Gairdner B. Momen. D. Appleton-Century Company, New York and London. \$4.00. 8½ x 5½; xix + 661; 1942.

The author has written this text with three principle aims in view: to present the material in as clear and logical a way as possible; to give the evidence for the conclusions that are made; and to show the human significance of the subject. These aims are excellent and in many respects the book lives up to them. It devotes considerable space to the experimental evidence, giving space to newer work as well as to the older, classic cases. The historical development of many of the subjects is worked in as an integral part of the text. The functional aspect of biology is emphasized, though morphology is not neglected. An extensive glossary and numerous excellent illustrations add greatly to the clarity of the text.

In many respects then this is an excellent book so that it is to be regretted that it does not always live up to the author's aim of clear presentation. Particularly in the early chapters, concepts and terms are introduced for which the student has not been adequately prepared, and the explanations of these are often far too brief. In several places examples are introduced to make a certain point clear. However, these examples are often ones which would be familiar only to the trained biologist. Not infrequently the present reviewer had the impression that the author was writing with his professional colleagues in mind rather than the student. If somewhat less material were introduced and more fully explained, the reviewer believes that the student would be less likely to be left floundering in a maze of unfamiliar ideas.

The general plan of the book is good. It starts with discussions of the science of biology in general and the universal characteristics of living things. Several chapters are then devoted to plants, including structure,

physiology, and reproduction. Following this, ecological relationships of plants and animals are considered. Then come a number of chapters on animal morphology and physiology including nervous and hormonal coordination. The more general biological problems of reproduction, development, heredity, and evolution are then discussed. The last two chapters are a history of life on the earth and a fairly detailed review of the phyla of the animal kingdom. Lists of "Useful References" are given at the end of each chapter and there is an extensive index.



BRITISH GRAHAM LAND EXPEDITION 1934-37 SCIENTIFIC REPORTS. Volume I, No. 8, *Tidal Observations in Graham Land. Part I*, by Brian Roberts; *Part II*, by R. H. Corkan; No. 9, *A Bibliography of Antarctic Ornithology*, by Brian Roberts. Also *Contents and Introduction; British Graham Land Expedition, 1934-37, Scientific Reports, Volume I, Nos. 1-9.*

The British Museum (Natural History), London. No. 8: 1s., No. 9: 2s. 6d. 12½ x 9; No. 8: 327-335, No. 9: 337-367; Contents and Introduction: 6; 1941 (paper).

These two numbers conclude Volume I of this important survey (cf. Q. R. B., Vol. 16, p. 489 for nos. 1-6). Number 7 describes the two automatic gages used in making tidal observations and discusses the reduction of the tidal observations of the present expedition to Graham Land and of the expedition in 1920-22. Information is also given on tidal data of Drake Strait. Tables and text figures and a map form part of the report.

Concerning the bibliography of antarctic ornithology Roberts says:

It is still too early to make the publication of such a work profitable. With the present taxonomic confusion, even the compilation of a list of species recorded from this interesting region presents serious difficulties. No adequate series of antarctic or sub-antarctic specimens, representing forms from the entire breeding range of a single genus, have yet been brought together; and if all existing collections were to be combined, they would still be quite inadequate for the purpose. Recent studies have revealed intricate diversity among certain groups, while others appear to have an extremely wide distribution without exhibiting any marked geographical variation. A sound classification of antarctic birds must await the collection of very many more specimens.

For the above reasons Roberts confines himself to providing necessary material for future work. He gives (1) a list of antarctic expeditions, with observers and collaborators who have published ornithological results (this aims to include the ornithological results of every antarctic expedition up to 1940); (2) publications listed in (1); (3) miscellaneous publications based on

museum and literary research; and (4) an index of localities.

For those who have the previous numbers of this fine survey—probably the last of its type for many years to come—a table of contents and introduction are provided.



A SYMPOSIUM ON HYDROBIOLOGY.

By Various Authors. *The University of Wisconsin Press, Madison.* \$3.50. 9½ x 6; ix + 405; 1941.

It is truly fitting that one of the recent very important contributions to the science of hydrobiology should come, in the form of the present *Symposium*, from the University which has done so much to advance that science in our country.

The scope of hydrobiology has, in the past few years, become so great that investigators in the field have been forced to make extensive use of chemistry, geology, and physics in order to solve their many problems. The present *Symposium* emphasizes very well this trend. The various papers deal with sedimentation, the rôle of dissolved gasses and of treated and non-treated sewage on various aquatic organisms, methods of chemical treatment of natural and artificial bodies of water, the rôle of sky and solar radiation in the determination of lake populations, and the relation of hydrobiological studies to problems of hygiene and sanitation. The volume brings out the breadth of the field which is included under the term hydrobiology and shows how important economically such studies are. Abstracts of papers presented in a volunteer program are included.

The *Symposium* is well edited and the papers are carefully written and adequately illustrated. It is impossible to pick out any one paper which is worthy of special note since each covers its topic adequately and, most important, each presents several unsolved problems in such a manner as to stimulate further investigation. It is unfortunate that no index has been provided.



BOOK OF BAYS.

By William Beebe. *Harcourt, Brace and Company, New York.* \$3.50. 8½ x 5½; xviii + 302; 1942.

A popular account of the second voyage of the yacht *Zaca* which carries us on a leisurely journey along the 3000 miles of the Pacific Coast from Lower California to the shores of Colombia. Beebe's ability to infect the reader with something of his own never-ending curiosity and boundless enthusiasm concerning the lives of animals of all kinds, including the human animal, is well exemplified in this book, and his brief pictures of such diverse subjects as the homing instincts of limpets, the iridescent colors of the boa constrictor and the joys of

circus day in Salvador, make entertaining reading indeed. The critical zoologist must take exception to some of the broad generalizations contained in the introductory chapters on the evolution of aquatic animals and to the misuse of some technical terms, such as the reference to the existence of "gills" in the human embryo and the use of the term "cetaceans" to designate the sea-lions. The layman, however, will leave the book with an increased knowledge of some of the problems with which the biologist is concerned and an added interest in natural history.



THE OPEN BOOK OF WILD LIFE. *An Introduction to Nature Study.*

By Richard Morse. *With a Foreword by David Seth Smith. The Macmillan Company, London and New York.* \$3.00. 8½ x 5½; viii + 240 + 16 plates; 1941.

Natural history and evolution are the keystones around which this treatise on British fauna and flora is built. The work is intended primarily for popular consumption, and as such presents the human interest side of biology in a very logical manner and in non-technical terms. Particular emphasis has been placed upon the social life among the lower forms, and the means whereby they meet the hazards of their natural environment and hence insure their own individual survival as well as the survival of the race.

The work is illustrated with a number of excellent line drawings and photographs (some in color), and is carefully indexed. In the hands of British nature lovers, the volume should prove to be a worthwhile contribution.



A NATURALIST IN CANADA.

By Dan McCowan. *The Macmillan Company, Toronto.* 15s. 8½ x 5½; xii + 284; 1941.

This book consists of a series of disconnected essays on various matters that come to the attention of the field naturalist. Not only do the habits and appearance of plants and animals figure in it, but also such related subjects as geology, folk-lore, the age in which animals live, the melting of the glaciers, forest fires, etc. The book is not only good natural history, but also good literature. It is illustrated with numerous photographs by the author, and two humorous drawings contribute not a little to the reader's enjoyment.



UNIVERSITY OF WASHINGTON PUBLICATIONS IN BIOLOGY. Volume 10, Nos. 1, 2, 3. *The Coleoptera of Washington. Carabidae: Agonini*, by Barbara Gray

and Melville H. Hatch; *Sphaeriidae and Histeridae*, by Rita Margaret McGrath and Melville H. Hatch; *Buprestidae*, by Frank M. Beer and Melville H. Hatch. University of Washington Press, Seattle. \$1.50. x 7; 144; 1941 (paper).



HUMAN BIOLOGY

SEA OF CORTEZ. *A Leisurely Journal of Travel and Research with a Scientific Appendix Comprising Materials for a Source Book on the Marine Animals of the Panamic Faunal Province.*

By John Steinbeck and Edward J. Ricketts. The Viking Press, New York. \$5.00. 9½ x 6; x + 598 + 40 plates + 2 charts; 1941.

FORGOTTEN WATERS. *Adventure in the Gulf of California.*

By Randolph Leigh. J. B. Lippincott Company, Philadelphia. \$3.00. 9 x 6; 324 + 24 plates + 2 maps; 1941.

After an unmerited neglect of about two centuries, one of the world's romantic bodies of water is being discovered anew. The "Vermilion Sea" (so-called on account of the great quantity of plankton in its upper reaches) differs in many ways from most other bodies of water. It is one of the very few gulfs without a bar at the entrance, but notwithstanding this it has a well marked *seiche*, the greatest tide-fall in the Pacific, and one of the greatest tidal bores in the world. It has one of the richest and most diversified marine faunas known (the town of El Mulegé would be an ideal site for a laboratory of marine biology) and at Cape San Lucas the boundary between the Californian and Panamic provinces is almost as sharply discontinuous as Wallace's Line in the East Indies. Nowhere else in the world except possibly at Bermuda, is the influence of the tropics felt so far north. The pearl industry of La Paz is second only to that of Manila, and cannibalism continued on Tiburon after Thackambau had suppressed this practice in Fiji.

To those who are imbued with the spirit of Kipling's poem about the explorer whom an inner voice impelled to search for something lost behind the ranges, the Gulf holds up a beckoning finger and a "come-hither look in the eye." Nowhere is the sea water more transparent than off the coast of Cochise, nowhere are the sunsets more brilliant than at Bocochibampo, and nowhere are the stars so bright or so numerous as in the sky of the Sonoran desert, fifty odd miles from the nearest water hole.

The recorded history of the gulf begins with the rivalry between Cortés and Mendoza, both of whom sent expeditions to its head waters to look for the Strait of Anian, a mythical channel thought to communicate with Puget Sound, thus making California the world's largest island. Although neither one found the strait, neither one could convince the European cartographers

of its non-existence, and it continued to appear on subsequent maps until 1701 when Padre Eusebio Kino, the missionary who made history as a by-product, completed his journey by land from Pimería Alta (Arizona) around the end of the gulf, demonstrating conclusively the peninsularity of Baja California.

Steinbeck's story of the expedition which he and Ricketts led into the gulf in search of biological material reads like one of his novels. The narrative of adventure holds the attention of the reader by his descriptions of the small boys who swarmed over their boat at every port, trying to earn a few centavos by bringing specimens, the officials who stared at their impressive looking documents without quite understanding them, the shiftless Seri Indians completely deficient in that ferocity that characterized their ancestors, as well as by his vigorous account of the climatic vicissitudes through which they passed. But Steinbeck never forgot that the expedition was primarily for scientific purposes, and he did his share of turning rocks and gathering mollusks, worms, and echinoderms, incidentally lacerating his hands on the barnacles and toughening his epidermis in the salt water.

Ricketts is also an author of standing. He has contributed to this work a chapter of instructions to collectors, very helpful lists of species taken, and bibliographic references. No similar survey of this region has been undertaken since Johann Xantus stored his collections in Manzanillo and slipped through the blockading fleet of the French in a rowboat at night, to be picked up by a passenger boat on the open ocean the next day. It does not take much imagination to visualize the shade of this biological pioneer following the cruise of the *Western Flyer* with interest and sympathy.

The object of Leigh's expedition was to study the silt deposition of the Colorado. His conclusion is that in times past this was adequate to compensate for the erosion of the delta by the tidal bore, but that Boulder Dam has destroyed this balance, so that drastic steps must be taken to prevent the waters of the gulf from eventually submerging the Imperial Valley. This theory is not likely to meet with universal acceptance. In the past forty years no silt from above Boulder Dam has reached the delta, owing to the desilting dams at Parker and Laguna. Further, the peak load of silt that a stream can carry is a unique function of its velocity and flow volume, and normally these are such that the saturation of the water desilted at Laguna is restored above the delta. While Lake Meade was filling the flow volume was naturally reduced, and the head waters of the gulf doubtless did advance northward somewhat, but when Lake Meade had filled, the flow volume was restored. As the quantity of water removed for agricultural purposes is increased the flow volume will be diminished accordingly, but a perceptible reduction of siltation from this cause is probably a long way in the future.

But Leigh does not confine his book to his problem. He writes delightfully of the seven towns on the gulf shore, which he identifies with the Seven Cities of Cibola. His narrative of the voyages of Alarcón, Link, Consag, and the other pathfinders of early American history strikes fire from the imagination, though he is guilty of a *lapsus calami* in stating that Nuñez and Estebanco were killed by Indians at Culiacán. As a matter of fact, Estebanco met his death in Arizona while serving as guide for Marcos de Niza, while Nuñez returned to Spain and many years later explored the upper reaches of the Rio de la Plata.

There are a few other slips—such as the estimated tidal difference of 50 feet near Phillips' point, the inclusion of the seals among the Cetacea, and the statement that Guaymas is likely to supplant Hermosillo as metropolis of Sonora, when probably the reverse was intended. But these do not detract from the enjoyment that the reader will derive from the perusal of the book.

To those who enjoy travelling in unfrequented and unfamiliar places, but whom circumstances compel to remain close to their hearthstones, these books weave a magic carpet on which we may penetrate in imagination beyond one of the few remaining frontiers in North America—a frontier incidentally not far beyond our own borders. To all such a great treat is held in trust between the covers of these books.



PRINCIPLES OF ANTHROPOLOGY.

By Eliot Dismore Chapple and Carleton Stevens Coon.
Henry Holt and Company, New York. \$3.75. 9½ x 6½; xi + 718; 1942.

Anthropology as a science is scarcely one century old. In this country the term anthropology is applied to what in Europe is mostly called ethnology. For a long time this science concerned itself merely with the curious habits and queer handcraft of "primitive people." In the last few decades, however, the chief interest shifted to, and rapid advances have been made in, the analysis and understanding of man's behavior and social relations, including those of modern "civilized" races. In its most recent development, anthropology has come to be defined as the science of human relations. Individuals are grouped in familiar, occupational, and institutional groups through relations which are determined by our habits, by techniques, by adaptation to environment, and by symbols and conventions for transmitting information, all of which together form our culture. These relations change with time and have become steadily more complex.

Guided by the latest views of modern anthropology the authors of this scholarly work have succeeded in supplying a much needed, up-to-date and comprehensive textbook of "human relations", of great service to students as well as teachers. The book will also be very stimulating to historians and instructive for biologists,

interested in behavior. The authors have wisely limited their attention to facts directly ascertainable from observations and have selected and arranged their objective descriptions in a clear and orderly manner, leading to amply supported and often novel deductions.

The wide scope of the book is best indicated by naming some of the most significant titles in the table of contents: The comparatively brief first part attempts to explain at least some of the biological foundations of human relations, especially the physiology of emotions, the development of conditioning and of personality, etc. This rather ambitious introductory section contains a few claims with which not all neurologists and psychologists will agree. A second part of over 200 pages discusses environment and technology, in particular such topics as manufacturing, gathering, husbandry, transportation, and division of labor. A third part, of 188 pages, is devoted to the systematic description of the development of institutions, such as the many and often complicated aspects of the family, and the fascinating and at times disillusioning history of political, economic, and religious institutions. The last two parts, of 231 pages, consider symbols and human relations, discussing such varied matters as rites of passage, rituals, magic, language, art, games, warfare, money, and law. The last paragraph of the conclusions is especially timely and worth quoting here:

Because anthropology, as we have seen, regards man as a whole, it can provide a unifying center around which a science of human relations can grow. The technological problems which plagued the people of an earlier day, problems of food and shelter and health, of more efficient means of transportation and communication, have largely been solved. We can look forward to increasing technical triumphs provided we are able to master the maladjustments in human relations resulting from technological change. At the present time, little attempt is made even to use what we already know in dealing with such problems. Only when the science of human relations becomes as fully developed as the older natural sciences can we hope to eliminate sources of individual maladjustment, bring about harmonious relations between the many groups making up a single nation, work out more effective and democratic systems of government, and extend their sway to the relationships between nations. Only with such a science can the basic problem of our civilization be solved,—how to increase our human adjustment and at the same time to increase our technological efficiency.

The appendix contains an excellent reading list of 70 titles, a useful glossary, needed in view of the specialized definitions of many words not in common use, and a detailed index.



THE SOCIAL LIFE OF A MODERN COMMUNITY. *Yankee City Series. Volume One.*

By W. Lloyd Warner and Paul S. Lunt. Yale University Press, New Haven; Oxford University Press, London. \$4.00. 9½ x 6; xx + 460; 1941.

"Yankee City," the research site, is an old New England town, chosen for study because it is a well integrated community "where the various parts of society were functioning with comparative ease," it has a few industries and factories, is autonomous and not a satellite of a large city, contains a number of ethnic groups and has a population of between 10,000 and 20,000 (actually 17,000). The information for this volume and the five others contemplated in the series, was assembled by an elaborate system of interviewing, observing, study of newspaper items and genealogies, etc., over a period of 10 years.

A social hierarchy in this community was discovered to consist of six classes, with only 3 per cent of the population falling into the two upper, and 85 per cent being fairly evenly distributed into the three lowest. The upper-lower was the largest of all classes, the lower-lower the smallest of the three lowest. The sharp breaks in numerical and percentual size of the classes occurring at the junctures upper-middle-lower-upper and lower-middle-upper-middle are construed to indicate that "the movement into and out of the upper-middle class is relatively less than in the other classes." The upper-upper class had a higher than average proportion of men, with the other classes presenting a fairly even distribution with regard to sex ratios. Residence (location and kind), marital condition, number of children, property ownership, budget items, occupation, membership in clubs, lodges, fraternities and churches, education of parents and children, crime and delinquency, reading habits (kind and number of books, magazines and newspapers bought or read) and the use of the public library, movie attendance, the choice of doctor, lawyer and other professional services, and proportion of ethnic members, all appear to be influences in some way by class factors—not necessarily monetary.

The first half of the book is given over to a description of the method, a description of the town and its biological characteristics, and a series of "profiles" presenting composite pictures of members of the various classes and illustrating as well mobile processes, both up and down the social scale. The later chapters give statistical analyses of the class similarities and differences as exemplified in the items listed above.

This study is of interest not only for its findings but for the application to a modern civilized community of a method which was originally developed by the senior author for the study of the social structure of a primitive Australian tribe. The research was conducted by the Committee of Industrial Physiology at Harvard University.



THE SOCIAL ORGANIZATION OF THE WESTERN APACHE.
By Grenville Goodwin. *The University of Chicago Press, Chicago.* \$4.50. 8½ x 5½; xx + 701; 1942.
This is a solid, authoritative, and very obviously sincere

work with a richness of detail which adds rather than detracts from the flow of interest. Most of the material the author obtained from the Western Apache of Arizona themselves, while he lived among them. On the reservation he was able to acquire an intimate knowledge of the day-to-day functioning of the social structure and to listen as well to the stories of a number of old Apache men and women, some of whose lives covered nearly a century and who recalled happenings told them by their parents and grandparents. By the addition of material from documentary and historical sources, the author was thus enabled to trace and compare the social and economic organization of the Apache from the aboriginal life, through the period of early contact with the whites and the uprooting to government reservations, to their present mode of life in a modern reservation community. Reservation life has wrought changes in practically all of their social, cultural and economic institutions, customs, and rituals—kinship practices, marriage, death and burial, children's play, etc. The one exception appears to be religion, for although war chiefs have become a thing of the past, the shamans still function much as they did in pre-reservation days. Apparently the most that the Catholic and Lutheran missionaries have succeeded in doing is to confuse the Apache concerning beliefs in the hereafter. As one Apache put it: "Nowadays we believe that the good people go to a place above and the bad to a place below. No one has ever been to the place above and come back so we don't know just where it is."

Of particular interest are the analyses of the clan organization and kinship systems. These lead "to the definition of a new type of 'phratry' for this region in which clan groups are joined together in 'chain fashion' rather than being sharply segregated." The very detailed observations of the play activities and training of children in their social and cultural setting should be of particular value to students of child development.

Goodwin had planned a series of monographs on various aspects of Western Apache life. With his death at the age of thirty-three, before this book was published, American Anthropology lost a brilliant and promising member.



IRENE MOUND SITE, CHATHAM COUNTY, GEORGIA.

By Joseph Caldwell and Catherine McCann. *With a Section on Physical Anthropology, by Frederick S. Hulse. University of Georgia Press, Athens.* \$1.50. 10½ x 8½; xiv + 84 + 25 plates; 1941 (paper).

This is a report of the first extensive excavations of the Irene Mound Site, located five miles from Savannah, Georgia, on the western bluff of the Savannah river. The region was known to the early settlers, and since the civil war sporadic investigations have been carried on. Intensive work commenced during the depression as

part of the Archaeological Project of Works Project Administration.

The large mound from which the site derives its name is 15½ feet high and 160 feet in diameter. A smaller mound, the burial mound, 55 feet in diameter and 2½ feet high, is immediately to the west of the larger mound, the edges of the two overlapping. Two large burrow pits are nearby. Identification of the site with any particular group of Indians was impossible but there is evidence that the last occupation lasted almost to historic times.

The excavations showed that the site was occupied by eight building stages.

The most impressive feature of the Irene site was the large proportion of presumably ceremonial buildings and inclosures, and the relatively small number of possible habitations. Evidently the site was a political or ceremonial center or both for the population of a considerable area. Despite the apparent lack of housing facilities, the large amount of midden indicates that domestic as well as ceremonial activities were carried on.

On the basis of the pottery studies, two main ceramic periods are recognized, an earlier Savannah and a later Irene. The burial mound was begun sometime during the Savannah period. One hundred and six internments were found with many of the bones in good condition and suitable for measurement. A mortuary built during the Irene period was probably used as a repository. Bone measurements show that in their physical characteristics the inhabitants were American Indians similar to those in neighboring regions.

The report is well supplied with illustrations and plates, showing pottery, plan of the buildings, skulls, artifacts of bone and of flint. A bibliography is provided but there is no index.



THE HAITIAN PEOPLE.

By James G. Leyburn. Yale University Press, New Haven; Oxford University Press, London. \$4.00. 9½ x 6; x + 342; 1941.

The Republic of Haiti, one of the smallest of the Latin-American republics, holds much interest for the people of the United States. Its war of independence, fought only twenty years after our own, made it the second free state in the hemisphere and the first independent Negro state in the modern world. The recent nineteen-year American occupation of the country has resulted in a close relationship between the two republics. Unfortunately, however, the average American's knowledge of Haiti has been gleaned largely from sensational works of fiction concerning its early leaders and from over-dramatized accounts of its "Voodoo" practices. The book under review, according well with our present policy of good neighborliness, affords a clear, succinct account of Haitian life and customs without either sen-

sationalism or over-dramatization. The author, on the basis of a personal acquaintance with the country and a firm background of research concerning its history, here presents "a connected story of the growth of its social institutions out of the backgrounds of slavery and French colonial life" and "of the slow shaping of these institutions through the nineteenth century." The political history of the country is recounted in some detail and the influences exerted upon the social structure by the efforts of the great leaders of the early days—Toussaint L'Ouverture, Dessalines, Christophe, Pétion and Boyer—are critically evaluated. The evolution of the two great "castes", the élite as opposed to the masses, is followed and the lines of demarcation which separate them are traced to their origins. The backgrounds of the religious beliefs of the country, including "Vodun", and the domestic life and politics of the people are fully considered. A final section deals in a most enlightening manner with modern Haitian problems: problems of over-population, national health, and national education, as well as the more intimate problems arising from the "caste" system and present-day color barriers. There is a comprehensive bibliography and a well-planned index.

A scholarly and sympathetic account of the Haitian people, this book will be of the utmost value to all who are interested in our Latin-American neighbors, whether as serious students or as casual visitors.



PROBATION AND PAROLE PROGRESS. *Yearbook National Probation Association Nineteen Hundred and Forty-one. Current Opinion on the Treatment and Prevention of Delinquency and Crime. Papers Given at the Thirty-Fifth Annual Conference of the Association at Boston, May 29-31, and Atlantic City, June 2-4.*

Edited by Marjorie Bell. The National Probation Association, New York. \$1.25 (paper); \$1.75 (cloth). 9 x 6; 470; 1941.

It was in 1841 that John Augustus, a Boston shoemaker, bailed into his custody a poor inebriate brought before the Boston court and thereby gave impetus to the probation movement in the United States. Thus this yearbook, which is a compilation of papers presented at the 1941 meetings of the National Probation Association, appropriately opens with a section of papers on John Augustus, his successors, and a history of the development of the probation movement and the closely related service of parole in this country. The other papers are arranged into five sections. In "The offender in the making" some of the less obvious social causes of crime and delinquency are brought out. The increasing need for case and clinic work is the main theme of the sections on "Trends in juvenile court practices" and "Probation and parole case work," the latter being more concerned with the adult or the family as a

unit. In the group entitled "Aiding the adolescent" Fritz Redl gives a penetrating analysis of adolescent changes as a factor in delinquency, in which he stresses particularly the types of changes, psychological or environmental, which may act either to decrease or to foster chances at therapy. This section also contains three papers on the pros and cons of the Youth Correction Authority Act, and a brief survey of the set-up and procedure of the Borstal System in England and the United States. The last section "Utilizing group situations," again deals with work with children and youth and describes the experiences with a group of maladjusted school children in Buffalo, the Y Rangers Boys' Club in Westchester County, New York, and the citizenship training program of the Boston juvenile court.



FOUR YEARS IN PARADISE.

By Osa Johnson. J. B. Lippincott Company, Philadelphia. \$3.50. 9½ x 6½; 345; 1941.

Five hundred miles north of Nairobi lies Lake Paradise, so named very appropriately by the late Martin Johnson and his wife, who is the author of this book. At this remote and beautiful place the Johnsons had spent four years in recording by moving pictures the practically undisturbed local wild life.

The book tells of the hardships, risks and pleasures encountered in photographing the large game and the natives in the surroundings of the Johnsons' elaborate camp by the lake. Much of their interesting experiences and their many adventures in Africa had already been described in several previous books by Martin Johnson. The present volume by Osa Johnson devotes much space to a woman's interests and activities in a busy life in the wilderness. She recounts in detail how she created a comfortable home, a productive garden, an efficient kitchen, how she entertained guests, attended to her pets, and with it all found time to sit in blinds at night, observing lions and other nocturnal prowlers, or go hunting and fishing with varied success. There is much one can learn from these pages: What to do when an elephant is about to charge, that one is not always safe from lions when riding in a car—as the author found when she had to shoot one old male which sprang and fell across the hood with one foot through the windshield—that there is no such thing as the often-claimed "elephant graveyard," that porcupine quills are excellent for digging out jiggers from under one's toenails, how birds can be cooked to perfection, unplucked and undrawn, if baked in clay, and much other widely varying information.

The volume is enriched by numerous fine photographs showing African landscape, fauna and natives, as well as the author in many different poses and costumes. There is the usual glossary accompanying most recent

books on Africa and an index which is too brief for real usefulness.



THE PUEBLOS: A Camera Chronicle.

By Laura Gilpin. Hastings House, New York. \$3.00. 9½ x 7; 124; 1942.

Among the most fascinating chapters in American archaeology and anthropology are those dealing with the Pueblos and Cliff dwellers of our Southwest—chapters which cover a period of over a thousand years. The homes of these people have in many instances been remarkably well preserved, or could be restored with justified confidence. There were villages in the valleys very similar to the present day Pueblos' dwellings and there were clusters of houses and towers on mountain tops and in the sides of almost inaccessible cliffs, the houses at times five stories high and several hundred feet long, providing shelter for an aboriginal population much in excess of that of to-day. These homes were fashioned of local stones and timber with crude tools and without mortar, but they were built to endure and designed to harmonize with their environment to perfection.

This book is mainly a collection of over 70 varied and beautifully reproduced photographs, showing the homes of the early Pueblos and the country in which they lived, together with many views from the daily life of their present descendants. Each picture is accompanied by brief, yet ample and instructive comment. A small map is included, indicating the location of some of the more important Pueblo ruins and contemporary settlements. Visitors to New Mexico and the surrounding states will find this little volume a stimulating guide, and everyone interested in early Americans will be delighted with these well-chosen pictures of some of our most ancient as well as most beautiful historic monuments.



CULTURE ELEMENT DISTRIBUTIONS; XVII YUMAN-PIMAN. *Anthropological Records, Volume 6, Number 3.*

By Philip Drucker. The University of California Press, Berkeley. \$1.25. 11 x 8½; 91-230; 1941 (paper).

The aim of this study is twofold:

to present a series of comparable data on the "rancheria" groups of the southwestern United States as a part of the University of California program of the culture-element survey of western North America; and second, to establish the cultural position of these tribes in relation to those of neighboring regions. This set of lists is meant to tie in with three previously made: Gifford's survey of the Puebloan and Athabascan Southwest . . . , Stewart's southern Basin survey . . . , and the southern Californian survey by the present writer. . . .

Data are given from seven Yuman-speaking and four Uto-Aztekan groups. Information was obtained from individuals of these groups. In order to obtain a check on the reliability of this kind of information Drucker compared his data with available literature. He found "the amount of error is reasonably low (I should estimate about 5 per cent of the total entries), and this error is chiefly in matters of minute detail." Points of disagreement have been cited in section "Ethnographic notes on the element list."

The culture element distributions are arranged in tables under the following broad headings: subsistence, material culture, amusements, social culture, individual development, ceremonials, Shamanism, miscellaneous customs and beliefs.

These records form a valuable addition to ethnological data of a comparative nature on Southwestern Indian culture.



ETHNOGRAPHIC BIBLIOGRAPHY OF NORTH AMERICA.
Yale Anthropological Studies, Volume I.

By George Peter Murdock. Yale University Press, New Haven; Oxford University Press, London. \$2.00.

10½ x 8½; ix + 168 + 1 folding map; 1941 (paper).

The present bibliography dealing with aboriginal North America is part of a much larger bibliography that the author has been accumulating for many years past on primitive and historical cultures "with the object, partly of directing distributional and other studies in the classroom, partly of recommending library purchases, and partly of preparing for a projected study which later materialized as the Cross-Culture Survey at the Institute of Human Relations." Murdock has provided teachers and students and especially field workers with a source book of great usefulness.

The plan of classification has been followed which modern anthropologists have found most satisfactory, namely by tribal groups, with an arrangement as a norm

the nationally self-conscious tribes of regions with some measure of political development, e.g., those of the Plains. For regions with less extensive political integration, groups of approximately the same degree of linguistic and cultural homogeneity were formed by arbitrarily uniting a number of tribelets or local groups, usually under the name of one of them.

Fifteen geographical areas are recognized for all of North America as far south as Tehuantepec, with the tribal groups numbering 277. A carefully-prepared, loose folding map shows the distributional areas.



INDEX OF THE AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY. Volumes I-XXII; 1918-1937. Part Two: Literature. Instituto Panamericano de Geografía e Historia, Publicación Num. 45.

Compiled by W. Montague Cobb under the direction of Aleš Hrdlička. Antigua Imprenta de Murguía, Mexico, D. F. 8½ x 6½; 394; 1941 (paper).

The rapid growth of the world's scientific literature makes it steadily more difficult to know what has become known, to use what information is available and thus to benefit fully by the labors of one's past and present colleagues. Our technical journals with their wide-ranging contents would become mere burial places for newly gained knowledge without an adequate index for finding readily everything that has been recorded in their pages.

Cobb has performed a labor of love in undertaking the arduous task of indexing in great detail the first twenty-two volumes of the *American Journal of Physical Anthropology*. The previously issued part of this index dealt with the original contributions in the Journal. The present, second part is devoted to the reviews in the journal of original papers published elsewhere. These reviews, which had been selected quite at random, are unfortunately very far from representing the world's contemporary literature on physical anthropology. The latter has been covered much more completely in several other journals, at least as far as listing titles and classification of contents is concerned. The usefulness of this index is also impaired by the fact that quite evidently there has been no proofreading, since printer's errors in foreign-language titles occur with intolerable frequency. In one instance there are nine errors in one title and it is difficult to discover the true meaning.



NORWEGIAN-AMERICAN STUDIES AND RECORDS. Volume XII.

By the Norwegian-American Historical Association.

Norwegian-American Historical Association, Northfield, Minnesota. \$2.00. 9 x 6; vii + 202; 1941.

Nine articles by as many authors are included in this book dealing with various social and cultural aspects of Norwegian-American history. The papers which probably will be of most interest to the sociologist or human biologist are the first two, in which change in surnames and the development of the Norwegian folk narrative in America, respectively, are utilized in tracing the migration of ideas and traditions from the Old World to the New. The other articles are more in the narrative or reminiscent manner. Two describe emigrant voyages in the 1840's and 1850's. There is one article on the pioneer life in Texas and two on the founding and development of the Norwegian-American press. Another chapter, by a life-long friend of Ole Edvard Rølvaag, is devoted to interesting recollections of the background and boyhood in Norway of the author of "Giants in the Earth." The last article is also biographical. It tells the story of Ole Evinrude and the outboard motor. Appended is the most recent install-

ment of a series, compiled for the Norwegian-American Historical Association, of publications by, about, or of interest to, members of the Norwegian element in the Americas.



OZARK COUNTRY.

By Otto Ernest Rayburn. Duell, Sloan and Pearce, New York. \$3.00. 8½ x 5½; ix + 325; 1941.

Rayburn prefers to restrict the Ozark country to the highland region of the southern half of Missouri, the northwestern part of Arkansas and a few counties in eastern Oklahoma. This empire of hills and valleys and occasional stretches of rolling prairie occupies an area approximately 60,000 square miles. Of the nearly one million people living in this region only about one-fifth live in the cities and larger towns, another fifth in the "favored rural sections" and the remainder in regions where they "must struggle against adverse economic conditions." This last group has, more than the others, lived in a world apart and has preserved the speech and customs of the early pioneer settlers. Here Rayburn finds the richest material for his book. He has given us a rather full and picturesque account of the family life and customs of these more secluded hillmen of the Ozarks and recorded it with sympathy and real understanding. He is particularly well fitted for the task, having spent much of his life in close association with these people. Ozark Country is the fourth of the American Folkways books edited by Erskine Caldwell.



FROM CRETIN TO GENIUS.

By Serge Voronoff. Alliance Book Corporation, New York. \$2.75. 9½ x 6½; 281; 1941.

This book, designed for popular consumption, represents an effort to delve into the nature of that rare phenomenon, a genius. The author is known for his discovery of rejuvenation through the process of grafting monkey glands in the human body. The "creative process" and the origin and "struggles" of genius are considered as manifested in certain great men throughout history, e.g. musicians, scientists, mathematicians, poets, artists, philosophers, etc. Many interesting anecdotes are related, each as illustrative of some particular point; documentation, however, is regrettably lacking. Because of the author's complete lack of emphasis on the rôle of the environment in developing the outward manifestations of inborn hereditary aptitudes, the impression is gained that environment has little or no influence. There are, furthermore, many loose statements, such as the following: "Genius possesses not only wondrous aptitude, it is simultaneously

endowed with *knowledge* which heredity, often a distant heredity, has bequeathed to it."

From Cretin to Genius makes the mistake often made by books dealing with the sensational. It tries to be sensational itself.



DEAD MEN DO TELL TALES.

By Byron de Prorok. Creative Age Press, Inc., New York. \$3.50. 9½ x 6; xiii + 328; 1942.

This is not so much the tale of dead men as it is the tale of live men—the primitive, savage, bestial, very-much-alive natives of Central Africa. Although the author began his trip through Egypt and Ethiopia with the aim of studying prehistoric cultures at various excavation sites, he seems to have been lured on to find out more and more about the primitive cultures of contemporary Africa, and less and less about prehistory.

The author's eye-witness accounts of the ceremonial practices of many dark and secret cults in the heart of Africa; his hair-breadth escapes from the jaws of certain death; and his glowing descriptions of the fauna, flora and terrain of equatorial Africa contribute alike to the suspense of this fascinating story. The modern version of African slave trading, and the political turmoil resulting from the attempted European domination of Ethiopia seem to have impressed the author as much as his prehistoric finds. In the field of pure adventure, the book contributes considerably more than in the field of archaeology.



STUDIES AND ACTIVITIES IN BIOLOGY.

By Chapin W. Day and Margaret Ritchie. Edited by John W. Ritchie. World Book Company, Yonkers-on-Hudson, N. Y. 80 cents. 10½ x 8; vi + 218; 1942 (paper).

This study and laboratory guide has been designed to accompany Ritchie's *Biology and Human Affairs* (cf. Q. R. B., Vol. 17, No. 1) for high school students.

The emphasis here is to get the biology class away from a checking of facts to a discussion of ideas and principles and their application in the world in which the student lives. A variety of experiments and activities are outlined, in completing which students will deal first-hand with a wide variety of living material. All are pointed to an understanding of biological principles.



BULLETIN DER SCHWEIZERISCHEN GESELLSCHAFT FÜR ANTHROPOLOGIE UND ETNOLOGIE 1941/42. 18. Jahrgang. Containing the following papers: *Vom Charakter des höchsten Gottes der Azteken*, by Hans Dietschy; *Die Skelettfunde von Holderbank im Kanton Solothurn*, by

Lucia Graf; *Skelette von Bonadus aus dem Ausgang der La Tène-Zeit*, by Otto Schlaginhaufen.

Edited by Otto Schlaginhaufen. Bückler and Compagny, Bern. 9 x 6½; 21-69 + 8 plates; 1942 (paper).



ZOÖLOGY

THE PIGEON.

By Wendell Mitchell Levi. With a Preface by Oscar Riddle. R. L. Bryan Company, Columbia, S. C. \$10.00. 11 x 8½; xxxii + 512 + 2 colored plates; 1941.

This book is written by a lawyer who "since early boyhood has raised pigeons and found in them a hobby which has brought relation coupled with stimulation to such a degree as to color and enhance every phase of my life." This quotation sets the spirit of the book. From the first chapter on the reader is filled "with the desire to learn more about a bird, which unlike any other single living creature, has won the interest, affection and veneration of mankind throughout the history of civilization." The pigeon is the emblem of peace as well as an effective means of liaison in war! Of all birds, according to a Philippine legend, only the dove understands the human tongue.

The second chapter, the longest in the book, deals with the breeds and varieties of pigeons and their probable origin. To all, except the pigeon fancier, their great number is impressive—almost equal, it would seem, to the number of breeds and varieties of the domestic fowl.

The chapters on anatomy and physiology are overflowing with information yet contain little of the more strictly technical literature on these subjects. Among the most interesting topics considered are how pigeons drink, whether each pair of eggs in a clutch produces a cock and a hen (a popular belief for over 2000 years), and the function of the ductless glands, particularly the hypophysis.

Chapter V first traces the origin and progress of the science of genetics—variation and inheritance. This is followed by an extensive list of familiar names of men who have made contributions, theoretical or experimental, to pigeon genetics. The more technical phases of the subject are dealt with quite adequately by the author. These include inheritance of color and morphological characters, such as "crest and hood," silky feathering, scraggly, webfoot and clumsy, and sex linkage. The chapter ends with a useful table of genetic characters.

The problem of pigeon behavior is treated in a somewhat popular manner, owing largely to the fact that the behavior mechanisms are not too well understood. Descriptions are given of the phenomena of courtship,

mating for life of cock and hen, nest-making, sense of location and homing ability.

The last six chapters deal respectively with Practical breeding, Diseases, Parasites and pests (their treatment and control), Feeds and feeding, Housing (ancient and modern), Commercial squab production, and The pigeon fancy (exhibition, racing, training, organizations, etc.). The book ends with an extensive bibliography and a complete index.

Considered as a whole the book is a fascinating one, combining both popular and technical information. It will appeal to the pigeon fancier and the layman, and to the scientist who needs to know much about pigeons before experimenting on them.



LICE. *British Museum (Natural History) Economic Series No. 2A.*

By John Smart. *British Museum (Natural History)*, London. 6d. 8½ x 5½; 32; 1942.

This pamphlet, listed in the "Economic pamphlets, dealing with the application of natural science to practical affairs," has probably been issued with the purpose of making available to the English people the best means of combating a pest which can easily be acquired under the crowded conditions of bomb shelters or unusual living conditions such as exist in England today. It is remarkable for its clear and simple style and interesting manner of presentation.

The different kinds of lice are distinguished, but chief attention is given to the three kinds of lice infesting Man (head, body, and pubic). While head and body lice have distinguishing characteristics, the two forms can be interbred. When head lice are bred continuously for several generations on the body they tend to assume the characteristics of body lice. It would seem that "Head and Body Lice are but two extremes of one species and that examples showing intermediate grades may occur."

Clear descriptions are given of the life history of the three kinds of lice of which man is host, manner of infestation, and the effects of habits of the host. Some individuals who are insensitive to lice may act as carriers. Three diseases are borne by the louse: (1) Typhus which is found in many parts of Europe, particularly Eastern Europe; it occurs in the United States in a mild form known as Brill's Disease; (2) Trench Fever which appeared during the 1914-1918 war, mainly among soldiers, but disappeared after the war; and (3) Relapsing Fever which is widespread but seems to be absent in Western Europe and the United States.

The last part of the pamphlet is devoted to the prevention and treatment of lousiness. With due regard to the desire that some readers may have to pursue this subject further Smart has provided a brief bibliography.

A FISHERY SURVEY OF IMPORTANT CONNECTICUT LAKES. *Bulletin No. 63. 1941. State of Connecticut Public Document No. 47.*

By the State Board of Fisheries and Game Lake and Pond Survey Unit. State Geological and Natural History Survey of Connecticut, Hartford. Free in Connecticut; \$1.00 outside of Connecticut. 8½ x 6; 339; 1942.

This report presents the results of a fishery investigation of 47 Connecticut lakes and ponds, and includes data gathered over a period of three years (1937, 1938, 1939). The purpose of the Connecticut lake and pond survey has been to gather fundamental information on the physical, chemical, and biological conditions in each body of water; to secure knowledge of the life history and habits of each important species of fish; the kind, extent, and probable effect of fish parasites; as well as other biological data. Numerous ways and means by which fishing may be improved are presented. Since the aim of the report is partly to give informative items of particular interest to sportsmen, the language used has been kept as simple and non-technical as possible.

The material discussed in the survey includes: management methods as applied to pondfish restoration, the lake as an environment for fish, procedures in a limnological survey, the life histories of various Connecticut fishes, the food and the growth of fishes, parasitism and the fish crop, and parasites in some Connecticut fishes as compared with other states. The appendix contains helpful information on: pondfish stocking, technical and analytical methods, and a summary of information and recommendations for the improvement of fishing. Extensive lists of the literature cited have been placed at convenient points in the book. The report is well illustrated with numerous photographs, drawings, and tabular and graphical material but there is no index. Much of the information herein presented will be of practical value in any region in the United States.



THE SEASONS AND THE FISHERMAN: A Book for Children.

By F. Fraser Darling. Illustrated with Drawings by C. F. Tunnicliffe. Cambridge: at the University Press; The Macmillan Company, New York. \$1.75. 8½ x 6½; viii + 70; 1942.

The author of this book has a story to tell and knows how to tell it. Although his language is so simple that any child could read and understand it yet it is not in any sense childish language. If an adult should read the book to a child their enjoyment of it would be equally divided.

The author has done a great deal more than merely follow the fishermen through the year. He explains why certain fish appear only in certain seasons, and this involves a discussion of "food chains," and the opening

chapter which deals with these covers the evolution of the sea and its plankton and is just as well written as the rest of the book. Also, the story of the deep sea fish, which the ordinary fisherman never sees, the life history of the eel, about which he knows nothing and cares less, and the ichthyologist's method of determining the age of a fish by examining its otoliths add much to the interest of the story.

Finally, one must add a word of appreciation of the preface. Some children seem to go through a period of development in which they seem to enjoy inflicting pain on animals. It is difficult to explain to such children why they should not indulge in cruelty when they see how it is involved in gathering food for mankind. But it is difficult to imagine any one reading this preface and not feeling more kindly disposed toward the animals of the sea.

The typography of this work is superior to the average and the artistic illustrations are superb.



BEETLES OF THE GENUS HYPERASPIS INHABITING THE UNITED STATES. *Smithsonian Miscellaneous Collections, Volume 101, Number 6. (Publication 3642.)*

By Th. Dobzhansky. Smithsonian Institution, Washington D. C. 35 cents. 9½ x 6½; 94 + 6 plates; 1941 (paper).

The ladybird beetles of the genus *Hyperaspis* are herein completely revised and new forms are described. No extensive work on this genus has been attempted since the publications of the late Colonel Casey who described well over half of the species. A large number of Casey's descriptions are now relegated to synonymy but the great majority are shown to be valid. Whenever possible, the genitalia were examined to establish specific distinctions.

The center of dispersal of this generic group was in Central and South America, whence it has spread to the South and Southwest of the United States. As a result, the majority of the forms are found in this area and only a few have reached the eastern and northern boundaries of the country. The writer holds that his results are still tentative because of the lack of specimens from the center of dispersal, but as far as actual specimens will permit him, he recognizes 72 species, of which eight are new; 31 subspecies, 11 of which are new; and six varieties, three of which are new; grouped into 14 (13 in the text due to a typographical error) categories of closely related species.

Each form is described, genitalia included whenever known, and the geographic distribution carefully listed. There are six plates which give details of the structure of the genitalia and of the elytral patterns. Many of the species are economically important as predators on scales and other insect pests, consequently such a thor-

ough revision of one of the largest and the least known genera in the family Coccinellidae is of considerable value.



COLLEGE ENTOMOLOGY.

By E. O. Essig. *The Macmillan Company, New York.*
\$5.00. 9½ x 6; vii + 900; 1942.

Insects play an important part in man's economic life. While some are destructive and the bearers of disease, by far the greater number are important in many ways, directly and indirectly, for man's existence, besides being of great biological interest. In the cross-pollination of plants they play an important rôle, they furnish food for birds and fishes, and they even are destroyers of obnoxious members of their own group.

To those acquainted with Essig's *History of Entomology* and *Insects of Western North America* this volume requires no introduction. Although much broader in scope than the latter book, by no means have all the half million described species of insects been included. The selection has been made on the basis of long association with the human race, some peculiarity in form, size, color or habits, and interesting and typical examples of family. The present volume has been written as a text, on traditional lines, but Essig has succeeded in making it extremely interesting. The volume has a wider usefulness, however, than in the classroom. The layman, with an interest in natural history, particularly in insect life, who lives or travels in out of the way places would do well to include the volume in his library, however limited that may be. The arrangement of the keys is excellent and easily mastered; the 308 figures are carefully chosen and well executed. Selected references accompany each chapter and a general bibliography and indexes of authors and subjects are provided. At the back is given a map of the zoogeographical regions of the world.



A MONOGRAPHIC REVISION OF THE MEXICAN WATER BEETLES OF THE FAMILY ELMIDAE. *Novitates Zoologicae, Volume 42, No. 2.*

By H. E. Hinton. *British Museum (Natural History), London.* 15s. 11½ x 7½; 217-396; 1940.

An unorthodox procedure in systematic entomology is used to define and distinguish the genera of beetles studied in this volume. Use is made of the internal anatomy of the alimentary canal, male and female reproductive organs, and the central nervous system. In most cases the anatomical studies show good correlation with external morphological criteria and in some where the latter fall down they reveal relationships not otherwise clearly understood. For instance, the genus *Cylloepus*, which seemed to consist of a homogeneous

assembly of species, is shown on the basis of the internal anatomy to consist of two very distinct groups. The external genitalia are also used to compare species. As a result of all this careful work most of the species are well allocated to their systematic positions.

Keys and complete descriptions make this monograph an exceedingly good one. The writer eschews comparative terms as "broader than long," "coarse," "fine," etc. Instead he uses actual measurements, even of the surface punctures; this procedure is to be highly recommended. Sexual differences are also described—a feature that is so often overlooked—and whenever known, the larval and pupal stages.

Statistical analyses of the measurements of the species were found to have limited application. Differences between two species were often less than those found in a single species at different altitudes.



THE PLANT BUGS, OR MIRIDAE, OF ILLINOIS. *Bulletin of the Illinois Natural History Survey, Volume XXII, Article 1.*

By Harry H. Knight. *State of Illinois, Urbana.*
\$1.25. 9½ x 6½; 234; 1941 (paper).

The Miridae, or plant bugs, rank as one of the most important groups of insects destructive to plant life in Illinois. Except for a few predacious species they suck the juices from plant leaves. Knight was put in charge of the survey which commenced in 1930 and continued through 1937. He identified the species and wrote the present report, but many others took part in the project.

The collection of Miridae numbered over 20,000 specimens and came from every part of the state. Collections were made at different seasons of the year over the same territory in order to get certain species which might be restricted to certain periods. The list of known Miridae of Illinois now includes 330 species, but since other species and varieties occur in the entire general region in which Illinois is situated and will probably find their way into the state, over 100 other species have been added to the list. In North America, north of Mexico, about 1500 species of Miridae are known.

Preceding the descriptive part, Knight devotes a section to the biology, distribution and habitat, preference, economic status and control, and taxonomy of the Miridae. The volume includes many excellent figures, a group of illustrations showing habitat, a list of host plants, a bibliography of 146 titles, and an index.



CATS AND ALL ABOUT THEM.

By L. H. Fairchild and Helen C. Fairchild. *Introduction by Belle J. Benchley. Orange Judd Publishing Company, New York.* \$2.00. 7½ x 5½; 231; 1942.

The authors of this book are a unique combination of cat lover and breeder and practicing physician and surgeon. They have recorded the results of their wide experience, with practically every breed of cat, with expertness and real understanding. The book is based to a certain extent upon the inquiries of hundreds of visitors to their cattery and as a result contains, along with the more intricate phases of care and management, those every day things about cats and kittens which writers so frequently take for granted and neglect to set down.

Topics such as successful methods of selection, breeding, management, housing, training and habits of cats are taken up in some detail. Descriptions of common ailments, their recognition and medication, together with the treatment for disease and parasites are also fully treated. Numerous photographic illustrations of various breeds of cats accompany the text.



REVISION OF THE NORTH AMERICAN MOTHS OF THE FAMILY OECOPHORIDAE with Descriptions of New Genera and Species. *Proceedings of the United States National Museum, Volume 90, No. 3107.*

By J. F. Gates Clarke. Government Printing Office, Washington, D. C. Free. 9½ x 6; 33 - 286 + 48 plates; 1941 (paper).

To the Oecophoridae belong several species that are of economic importance, some forms that feed on stored products, such as dried foods, bulbs and tubers, scavengers that feed on the refuse occurring in the nests of mice and birds, and forest forms that attack the beech, oak, pecan and hickory. The majority of the Oecophoridae are leaf and flower feeders in the larval stage.

In this revision are listed 22 genera and 117 species of which 6 genera, 19 species, and 1 race are new. Detailed descriptions are given for each form, place of type, type locality, food plants and distribution. A series of fine drawings (48 plates with 288 figures) illustrate distinctive features. An index to the genera, species, and localities is provided, also an index to food plants.



OUR AMERICAN GAME BIRDS.

By Van Campen Heilner. Foreword by Colonel Theodore Roosevelt. Paintings and Drawings by Lynn Bogue Hunt. Doubleday, Doran and Company, New York. \$5.00. 13 x 9½; xi + 178 + 19 plates; 1941.

As an account of the habits, migration routes, breeding and wintering grounds of the game birds of the Western Hemisphere this book serves its purpose as a reference work for the sportsman. Unfortunately its large size precludes its use as a field manual. There is some very

sound advice to the hunter concerning the haunts and habits of many of the birds listed which should aid him in obtaining his bag limit. There are nineteen color plates by Lynn Bogue Hunt. The extremely gaudy colors in the background of these paintings detract a great deal from the coloration of the birds themselves.

The appendix contains much valuable information about hunting dogs, bird flight and waterfowl regulations. There is also a useful field guide, and several maps showing the ranges and migration routes of many of the birds described.



WORLD OF BIRDS.

By Eric Parker. Longmans Green and Co., London and New York. \$3.00. 7½ x 4½; vii + 295; 1941.

To the very large number of popular books written about wild birds both in this country and England we have another to add. Since the subject matter of such books is very much the same (usually being a description of the appearances and habits of birds with which the author is somewhat familiar) originality of treatment is rare. Not so, however, with Parker's book. We have here a most refreshingly original treatment of English bird life written in a very personal style. Although the author is somewhat amusingly poetic in some of his descriptions, this in no way detracts from the general interest which the book will have for many readers. The accuracy with which the subject matter is treated and the critical attitude the author takes in his discussions of the habits of birds, about which different beliefs exist, are particularly commendable.



AMERICAN WATER BIRDS: Also Hawks, Owls and Game Birds.

By Maitland A. Edey. With Colored Plates by Louis Agassiz Fueses. Random House, New York. \$1.00. 11 x 8½; 72 + 29 plates; 1941.

This little book has been written as a companion volume to *American Songbirds* by the same author. Like the latter it has been prepared as an aid to those just starting on their study of bird life. The most valuable feature of the book is its twenty-seven colored plates of birds by the dean of all bird artists, Louis Agassiz Fueses. Considering the low price of the book, these illustrations are rather accurate reproductions of the original paintings of Fueses. Included with the plates are simple, accurate, though very brief descriptions of the birds and their habits. All of the familiar water birds of the Eastern and Central United States and Canada, as well as representative hawks, owls, and some upland game birds constitute the subject matter of the book.

THE FORAMINIFERA OF THE TROPICAL PACIFIC COLLECTIONS OF THE "ALBATROSS," 1899-1900. Part 3, Heterohelicidae and Buliminidae. United States National Museum Bulletin 161.

By Joseph Augustine Cushman. Smithsonian Institution, Washington, D. C. 20 cents. 9 x 5½; v + 67 + 15 plates; 1942 (paper).

A third part of a work describing and illustrating the Foraminifera of the tropical Pacific collected on the *Albatross* survey. Part 4 will complete the work and will take up in systematic order the families beginning with the Rotaliidae.

Cushman finds that the number of distinctive species in this area is large. "Some interesting relationships have been noted in these faunas in which are living representatives of species known hitherto only from the late Tertiary of other regions."

Twenty-nine tables give the locality, depth, bottom temperature, character of bottom, and occurrence. The 15 plates show many views of the forms described.



OYSTERS HAVE EYES: or the Travels of a Pacific Oyster.

By Eldon Griffin. Wilberlilla Publishers, Seattle.

\$1.00. Discount of 25 per cent in quantities of 25 or more. 9½ x 7½; 53; 1941 (paper).

Sifting through the verbiage of this popularized account of the Pacific oyster—the oyster is called Oliver—we find some interesting general information concerning oysters and the oyster business in the State of Washington. Apparently the oyster beds will suffer from the Pacific war since "the high-grade seed, or spat, on which the Pacific-Oyster industry depends for its life has come from Japan. Scores of Americans, particularly in the State of Washington, have invested hundreds of thousands of dollars in land and equipment for the use of which the supply of imported seed has been essential."



A LABORATORY MANUAL FOR ELEMENTARY ZOOLOGY.

By W. Byers Unger and C. E. Mority. Ginn and Company, Boston. \$1.25. 10½ x 7½; iv + 106; 1042.

This manual has developed out of a series of laboratory directions used in a one-semester, elementary course in zoology at Dartmouth College. Certain vertebrate systems—digestive, respiratory, and reproductive—are presented as demonstrations so that detailed laboratory instructions are unnecessary. A very good introduction to the use of the microscope is given and a glossary of terms frequently employed. Blank right-hand pages are provided for student drawings.



LABORATORY DIRECTIONS IN PRINCIPLES OF ANIMAL BIOLOGY. Fifth Edition.

By A. Franklin Skull with the Collaboration of George R. Larue and Alexander Ruitvoen. McGraw-Hill Book Company, New York. \$1.00. 9 x 6; ix + 102; 1942.

No fundamental change has been made in the present edition of this laboratory guide. In the main, the revisions have been made to conform to the changes in the recent fifth edition of *Principles of Animal Biology* (cf. Q. R. B., Vol. 16, p. 492) which the laboratory guide was designed to accompany.



OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN. Nos. 449-456. A Race of the Blue-hooded Euphonia from Sonora, by A. J. van Rossem; The Pygmy Owl of the District of Soconusco, Chiapas, by Pierce Brodkorb; Note on Salamanders with Descriptions of Several New Forms, by Sherman C. Bishop; Some New Snakes from Guatemala, by L. C. Stuart; A Race of Woodhewer from the Alto Parana, by Pierce Brodkorb; Geographic Variation in Mesogonistius Chelodon (Baird), with Description of a New Subspecies from Georgia and Florida, by Reeve M. Bailey; Descriptions of Two New Species of Plectrohyla Brocchi with Comments on Several Forms of Tadpoles, by L. C. Stuart; The Pleuroceridae of the Atlantic Coastal Plain, by Calvin Goodrich.

University of Michigan Press. Ann Arbor, Michigan. 9 x 6; No. 449, 2; No. 450, 3; No. 451, 21 + 2 plates; No. 452, 6; No. 453, 2; No. 454, 5; 1941: No. 455, 14; No. 456, 6; 1942. (Paper.)

DEVESCOVINID FLAGELLATES OF TERMITES. II. The Genera Caduceia and Macrotrichomonas. University of California Publications in Zoology, Volume 45, No. 2.

By Harold Kirby. University of California Press, Berkeley. \$1.00. 10½ x 6½; 93 - 166 + 12 plates; 1942.



BOTANY

A SHORT HISTORY OF THE PLANT SCIENCES.

By Howard S. Reed. Chronica Botanica Company, Waltham, Massachusetts; G. E. Stechert and Company, New York. \$5.00. 10½ x 6½; 320; 1942.

Volume VII of "A New Series of Plant Science Books," edited by Franz Verdoorn, is an account by Reed of the development of plant sciences from earliest records to the present time. The condensation of this enormous subject matter into a little over 300 pages is in itself an achievement. Reed, however, has succeeded far beyond this goal. He has presented in brief form not only historical accounts of the contributions of practically all principal botanists of the past but has included side-lights on their personalities and the general atmosphere of the times in which they worked.

The first chapter gives an outline of four stages in the

development of plant sciences from the period of "Accumulation" of information through "Verification" and "Classification" to the last period of attempted "Interpretation". Thus he traces the growth of botany from the times of isolated observations to the present trend of organization of plant sciences on an international scale.

The next seven chapters deal with epochs of progress and partial retrogression from civilizations of antiquity up through the Renaissance period with the rise of experimental, natural science in western Europe and its progress to the end of the 18th century. The attention to contemporaneous and earlier Asiatic, particularly Chinese, agricultural achievement and to the development of crop plants and gardening on the American continents is of special interest.

In his account of the tremendous advances since the beginning of the 19th century the author has fortunately chosen to present the subject matter in topic form. Chapters 9 to 19, inclusive, trace the developments leading up to and constituting the separate fields entitled: plant-geography, -morphology, -cytology, water economy of plants, the fixation of carbon, the assimilation and fixation of nitrogen, plant nutrition, mineral constituents in metabolism, mycology and plant pathology. These chapters are more than historical accounts of pioneering investigators and their findings. They form an integrated picture of what the main problems were, what has been accomplished and thus point the directions in which present work leads. They are written with a mature judgment of the subject as a whole and with an insight into functional relationships in plants rarely found associated with historical treatments. These chapters, therefore, contain descriptive material freshened with the experimental viewpoint and reflecting the vital qualities in botany to an extent which will stimulate interest and admiration on the part of uninitiated and advanced students alike. The text might have been further enlivened by a few representative experimental results shown in tabular or graphic form. The book does contain, however, 37 illustrations varying in kind from reproductions of early manuscripts, texts and drawings of plants and tissues, to etchings of some famous botanical institutions and gardens.

Naturally, as the author points out, it is not possible to cover all that has been accomplished in botany in a book of this size. The choice of material and topics has been guided by the author's own interests as well as by considerations of treatments already available on certain topics which have undergone recent and exceptionally rapid development. This has imposed certain limitations from the historian's point of view but has added unity and direction to the book, which to most readers will be far more significant and desirable. A list of references to original papers and to more complete treatises on specific subjects is appended to each chapter.

A distinctive quality of the book is its placing of em-

phasis. Scientific historical accounts are often of two extreme types. One is so noncommittal and unorganized that the average reader gets lost in technicalities. The other, popular, type exaggerates the importance of a few individuals upon whose shoulders is placed entire responsibility not only for ideas and generalizations but also for detailed elaboration of all accomplishments connected with their times. This procedure fails both on points of accuracy and continuity of progress. The present book strikes a happy balance between the two types. It conveys admiration and due credit to outstanding men but includes kindly rebuke for their shortcomings properly flavored by the author's own evaluation of specific contributions and contributors. The last chapter gives his list of 50 significant names in the history of botany judged on status as discoverers, classifiers, specialists and exponents of botanical knowledge. Most important in this connection is the fact that though the book deals mainly with individual contributors, the subject matter rather than personalities is the central theme throughout.

The book is intended primarily for the orientation of graduate students in botany. For this purpose it should serve admirably and will fill a great need. The simple style and treatment of a vast fund of information will recommend this book to a much wider audience as well.



A SYMPOSIUM OF THE STRUCTURE OF PROTOPLASM. *A Monograph of the American Society of Plant Physiology.*

Edited by William Seifriz. Iowa State College Press, Ames, Iowa. \$3.00. 8½ x 5½; vi + 283; 1942.

This volume represents the first of a series of monographs to be published under the auspices of the American Society of Plant Physiologists. As originally planned, the symposium, of which the present volume is a record, was intended to bring together biologists, physicists, and chemists in the discussion of protoplasmic structure. Although an unfinished paper by Freundlich and short communications by Astbury and Meyer are the only direct contributions by physicists and chemists in the strict sense, the influence of these fields is very evident in most of the papers of the symposium.

On a molecular level, papers by Moyer and Sponsler and Bath deal with the configurations found in protoplasm, and the forces that may be involved in the various types of aggregation observed. Actual experimental evidence in this field is not abundant, but some very promising studies have been made, particularly X-ray studies of the configuration of protein chains and the distances involved in various molecular arrangements. A large part of the monograph is devoted to various aspects of the sol \rightleftharpoons gel transformations so important in protoplasmic activity. In Freundlich's paper this

subject is taken up from the standpoint of the behavior of well-defined colloidal systems *in vitro*. This approach does much to clarify interpretations of observed protoplasmic behavior.

Kamiya, in an interesting paper, presents a method by which he has been able to measure the magnitude of the motive force producing protoplasmic streaming, a measurement which had not previously been made. He finds that this force fluctuates rhythmically, and by means of Fourier analysis he has been able to resolve the curves obtained into several harmonic components of suitable amplitudes and frequencies. Only a small amount of work has been done with this method, but the findings must be considered in any interpretation of the forces involved in protoplasmic motion.

This monograph is probably the most complete discussion of protoplasmic structure now available, and each paper is accompanied by a bibliography of pertinent literature, which adds to its value. In a few cases the picture may have been somewhat obscured by excessive reference to outmoded cytological data, but the general emphasis is on advanced physical-chemical methods which are the basis for so many recent advances in this field. As in any treatise which deals with the border line between established fact and theory, many hypotheses are advanced with little exact experimental backing. However, these represent the ideas of many of the foremost workers in the field, and should prove helpful in guiding further thought and experimentation on these problems. The book should be of interest and value to everyone interested in fundamental biological problems.



AN HERBAL [1525].

Edited and Transcribed into Modern English with an Introduction by Sanford V. Larkey, and Thomas Pyles. Scholars' Facsimiles and Reprints, New York. \$3.50. 9 x 5½; xxiv + 86; 1941.

Agnes Arber, in her interesting book, *Herbals: Their Origin and Evolution*, reviews the evolutionary period of the herbal, covering about 200 years (1470-1670) after the discovery of printing when there was much activity in the production of such works, many of them based on much earlier manuscripts. The present *Herbal* falls within this period. Arber considers it

"possible that this book may have some claim to originality but it is more probable that it is derived from an unknown mediaeval manuscript dealing with herbs." Larkey and Pyles believe that "[Eleanor Sinclair] Rohde probably comes nearer the truth when she writes, 'it gives the impression of being a compilation from various sources, the author having made his own selections from what pleased him most in the older English manuscript herbals.' . . . If the work has any single source, that source was itself ultimately a compilation, we may be sure, the compiler having taken what seemed to him good and useful wherever he found

it. There is, as a matter of fact, internal evidence of two different ultimate or immediate sources. . . ."

The *Herbal*, in quarto volume, in black letters, came from the press of one Richard Bankes—"Imprinted by me Richard Bankes, dwelling in London, a little from the Stocks in the Poultry, the twenty-fifth day of March. The year of Our Lord 1525." The first book appearing in England devoted exclusively to herbs, it bears on the title page "Here begynnnyth a newe mater, the whiche sheweth and treateth of ye vertues & propyrties of herbes the whiche is called an Herball." Only two known copies now exist; one in the British Museum, from which the Larkey-Pyles facsimile has come, and one in the Huntington Library, San Marino, California. Other editions followed the first issue and the volume was probably widely read and the countryside diligently searched for many plants that were not regularly cultivated.

The herbs are listed alphabetically in 207 chapters, each dealing with a particular herb. Some chapters are only one line in length, others run to two or more pages. The terms that seem to occur most frequently are "this herb is hot and dry", or "cold and dry", or "hot and moist", or "cold and moist." Mostly the virtues of the herbs are in their effect on the digestive tract and the internal organs, but the same herbs when applied externally, either alone or in mixtures, have the power to cure many ailments.

We quote briefly some of the methods of treatment which are given:

'Also, if this herb [wormwood] be pounded with the gall of a bull, and afterward put into a man's eyes, it putteth away all manner impediments of the sight.' ". . . take the flowers of rosemary and make a powder thereof and bind it to the right arm in a linen cloth, and it shall make thee light and merry. . . . Also, take the leaves and put them into a vessel of wine, and it shall preserve the wine from tartness and evil savor, and if thou sell that wine thou shall have good luck and speed [success] in the sale." "Also, the juice of onion tempered with any liquor is good to drink for any man that hath lost his speech." Mustard "comforteth the stomach" as it sometimes has in modern times.

The authors have produced a scholarly volume, thoroughly documented. It will interest botanists, herb growers, physicians, and the book collector.



CLIMATE AND MAN. *Yearbook of Agriculture, 1941.*

United States Department of Agriculture. Government Printing Office, Washington, D. C. \$1.75. 9 x 5½; xii + 1248; 1941.

Among the environmental factors influencing man's well-being, climate undoubtedly ranks first in that it determines his distribution and controls his movements over the earth's surface, it regulates to a great extent

his agricultural and industrial economy, and it confronts him with some of the greatest problems with which his ingenuity has to cope. Although man still abides by the profound observation of Mark Twain in that everybody talks a lot about the weather but nobody does much about it, the fact remains that he is now able, in some measure at least, to meet the hazards of flood, drought, dust storm, and other climatic aberrations as never before in the history of his race.

In this 1250-page treatise, the Department of Agriculture has brought together all the pertinent data concerning climate as related to agriculture in the United States. In the early sections of the book are found detailed accounts of climate and weather as they affect (1) our important fruit, forest, grain, truck, and livestock production; (2) the common diseases of domestic plants and animals; (3) soil and water conservation; and (4) flood control and irrigation farming. A short middle section of the volume is devoted to a discussion of the scientific basis of modern meteorology and weather prediction under such headings as wind directions, ocean currents, atmospheric pressures, cloud formations, and daily as well as long-range forecasting. The latter portion of the yearbook is concerned with (1) the climates of the world, and (2) the climates of the different states of the U. S. A. The discussions of the climates for each of the states include many maps and tables showing the mean monthly, the mean annual, and the average seasonal precipitation, the earliest and latest frost dates, and the average January and July temperatures for the various counties during the period in which weather records are available. Supplementary climatic notes for Alaska, the Hawaiian Islands, and the West Indies including Puerto Rico are listed.

Each topic of discussion throughout the book is well documented with references from the scientific literature, and is illustrated with a variety of well-chosen photographs, maps and line drawings. A complete index is appended.



THE BOOK OF TREES. *Second Edition, Revised.*

By Alfred Carl Hottes. A. T. De La Mare Company, New York. \$3.50. 7½ x 4½; viii + 440; 1942.

The Book of Trees is a new addition in the series of some 45 De La Mare Garden Books. As stated in the preface it "is intended for the amateur, the gardener and the nurseryman, but it makes no pretense of appealing to the foresters. The trees are discussed from the viewpoint of a horticulturist, not a botanist." Some 12 or more poems inserted in the text warrant the addition of the nursery-maid to the list of potential users. From a strictly scientific point of view the book offers little of value. The first 48 pages include brief discourses on such topics as "why plant trees?" and "the mystery of the autumn leaf." From the practical standpoint the book has much to recommend it. It contains helpful

directions for selecting, planting, pruning, grafting, transplanting, propagation of, and generally caring for, trees. Several lists indicating rapidity of growth and suitability of trees for different purposes and localities are supplied. The main part, some 250 pages, consists of detailed descriptions of important deciduous and coniferous trees. Descriptions of characteristics, habitat, utilization, etc., are provided together with key for identification. There are numerous photographic reproductions of both the trees and their flowers. Many of these are excellent. Also included in the 200 or more illustrations are some pen drawings of plant parts and many sketches of characteristic features—fruits, twigs, buds, leaf scars, etc.

The final chapter is a table of some 270 deciduous and 85 coniferous trees, listing scientific and common names and characteristics as to height, shape, color of flowers, fruit and special remarks.

The book may be recommended to anyone who has an active interest in home gardens or city beautification—in fact, to anyone who "takes joy in supplying a fit environment for a growth that approaches perfection."



A BOOK OF ROSES.

By J. Ramsbottom. *With Plates after the Originals in Redouté's "Roses".* Penguin Books Ltd. Harmondsworth, Middlesex, England; New York. 60 cents. 7½ x 4½; 30 + 16 colored plates. 1941.

One of the most famous of the scientific treatises devoted to the description of species and varieties of the rose is *Les Roses* by Pierre-Joseph Redouté (1759-1849) who has been called "le Raphaël des fleurs." Successively engaged in the decorating of churches and castles, in painting the portraits of the most prominent persons in Luxembourg, and in floral decorative painting, Redouté was appointed, in 1822, "maitre de dessin pour les plantes" at the Jardin des Plantes in Paris. There he continued to add to the collection of paintings of plants begun by Gaston d'Orleans in the seventeenth century, and introduced the method of employing water-color on vellum instead of the gouache customary at that time. It is estimated that, in addition to his other paintings, he painted over a thousand roses. Many of these were included in the three editions of *Les Roses* that appeared during his lifetime. Sixteen of the water-colors there published are beautifully reproduced in this book. The plates are preceded by brief descriptions and data on the origin of the varieties depicted. An historical introduction contains, in addition to a brief biography of Redouté, interesting comments on the rose in literature, its use in religious ceremonies of different peoples and in heraldry, and notes on the distribution and origin of some of the most popular varieties. The format is attractive and the book makes a nice appearance on the drawing-room table.

SEEDING AND PLANTING IN THE PRACTICE OF FORESTRY. *A Manual for the Guidance of Forestry Students, Foresters, Nurserymen, Forest Owners, and Farmers. Third Edition.*

By the Late James W. Toumey and Clarence F. Korian. John Wiley and Sons, New York; Chapman and Hall, London. \$5.00. 9 x 5½; xxii + 520; 1942.

Among the more significant advances that have been made in silviculture during the decade that has elapsed since the appearance of the second edition of this book (cf. Q. R. B., Vol. 13, page 238 for mention of the second edition) are the construction of well-equipped extractories and seed-storage plants, the mechanization of most of the major operations in seed extraction, and the establishment of huge nurseries, some of which have a capacity of several million trees. The material on these has been revised and expanded to include the most up-to-date methods. The chapter on "Planting surveys and plans" has been enlarged in view of the recently increased emphasis in the programs of federal, state and private agencies on the production of nursery stock for planting on particular sites. Throughout the book a number of small-scale and generally outmoded methods and practices which have rather limited application in the United States have been included for the sake of completeness. As in the second edition, time scales, rather than cost figures, for the various operations are given, as the cost is dependent somewhat on wage scales which vary from time to time and according to locality.

Common and technical names of trees mentioned in the text are listed in an appendix, and author and subject indices have been provided.



WEEDS.

By Walter Conrad Muenscher. *The Macmillan Company, New York.* \$4.50. 8½ x 5½; xxii + 579; 1942.

As in the three previous editions, the weeds (approximately 500 in number) described are indigenous to the northern United States and to Canada. The major portion of the book is a catalogue of the weeds, arranged in alphabetical order under their scientific names, by families. Each species or variety is described fully for purposes of ready identification. In addition information is included on its source and dissemination, type, geographic range, location and soil preferred, propagation, whether the weed is poisonous or harmful to stock, and specific directions for its eradication or control. The 123 illustrations show the whole plant and detail of root, seed, branch, flower and fruit of 320 varieties. There are four introductory chapters entitled, respectively, "The dissemination and importance of weeds," "Weeds of special habitats," "The control of weeds," and "Chemical weed control." These are followed by a key to the species, based primarily on flowers and

fruits which the authors consider "more constant than the vegetative organs and habits of weeds." The fact that three editions of this book have appeared since it was first published six years ago is evidence of its popularity and usefulness. The revisions made for the present edition are not extensive.



STANDARDIZED PLANT NAMES. *Second Edition. A Revised and Enlarged Listing of Approved Scientific and Common Names of Plants and Plant Products in American Commerce or Use.*

Edited by Harlan P. Kelsey and William A. Dayton. J. Horace McFarland Company, Harrisburg, Penna. \$10.50. 9 x 7½; xv + 675; 1942.

The first edition of this book, published in 1923, attempted to cover only the field of horticulture. The present edition has been prepared with other related interests in view, such as agronomy, farming, forestry, fruit-growing, gums and latex, pharmacy, spices and condiments, range and wildlife management and soil conservation. Approximately 90,000 separate entries of plant and plant product names appear—more than twice as many as in the first edition. Other innovations over the 1923 edition include: indications of pronunciation, the use of symbols to indicate clons, hybrids, polybrids, and plants useful to wildlife, and a glossary. The arrangement is alphabetical, in general by species, but includes also special plant lists such as drug plants, plants of significant economic use, poisonous plants, range plants, and state flowers and trees. The publication of this book will undoubtedly be most heartily welcomed by botanists, gardeners, nurserymen, pharmacists, librarians and editors.



FLORA ARTICA: BRYOPHYTA OF CANADIAN ARCTIC. *Collection of Father Arthème Dutilly.*

Identified and Annotated by William Campbell Steere. The Catholic University of America, Washington, D. C. 50 cents. 9½ x 6½; 1941.

This list of bryophytes forms a substantial contribution to our knowledge of Canadian flora. It represents painstaking and careful collecting and recording in many widely scattered regions in the Arctic. Father Dutilly, naturalist of the Arctic Oblate Missions, made the first collections in the summer of 1934 in the vicinity of Coppermine, Coronation Gulf and at Letty Harbour, Amundsen Gulf. Other summers he collected in the region west and north of Hudson Bay. The specimens were sent to various places for identification but by far the larger part have been identified by Steere and his co-workers. For each of the 163 forms there is a record not only of the collection number, date of collection, and local distribution but also of the distribution in larger,

natural geographical units, as follows: Labrador, Northernmost Quebec, West Side of Hudson Bay, Shore of Arctic Ocean, Melville Peninsula, Southampton Island, Baffin Island, North Devon Island, and Ellesmere Island.



TREES OF THE EASTERN UNITED STATES AND CANADA: Their Woodcraft and Wildlife Uses.

By William M. Harlow. *Whittlesey House, McGraw-Hill Book Company, New York and London.* \$2.75. 7 x 4½; xiii + 288; 1942.

This pocket-sized book is designed for the hiker, camper, or anyone who is interested in knowing our eastern trees. Following the introduction which contains a non-technical discussion of the terminology and a general key, each important tree is described under the headings: Appearance, Leaves, Flowers, Fruit, Twigs, Bark, Habitat, Distribution, and Remarks. Other trees belonging to the same genus are briefly and clearly described so as to be easily distinguishable. The book is thoroughly illustrated with clear photographs of leaves, twigs, flowers, fruits, bark, etc., so that identification is made as simple and painless as possible.

This field book should be welcomed by those who would know the trees yet possess neither the technical knowledge nor the urge to ferret out the meaning of the terms used by the botanical fraternity.



DESERT WILD FLOWERS. Revised Edition.

By Edmund C. Jaeger. *Stanford University Press, Stanford; Oxford University Press, London.* \$3.50. 8½ x 5½; xxx + 322; 1941.

A key, prepared by Ruth Cooper, for the quick identification of desert plant specimens and a glossary are included in this edition (cf. Q. R. B., Vol. 15, p. 489 for notice of the first edition). With these exceptions and a few corrections in the text there are no differences between the two editions of this beautiful and fascinating laboratory manual. In all, 754 plants of the California deserts and related portions of Nevada are described and illustrated by excellent line drawings (executed by the author) or photographs. The paper selected for this book is suitable for filling in the coloring on the line drawings with indelible colored pencils—from living specimens it is hoped.



MORPHOLOGY

INTRODUCTION TO VERTEBRATE EMBRYOLOGY. Fourth Edition.

By Waldo Shumway. *John Wiley and Sons, New*

York. Chapman and Hall, London. \$4.00. 9 x 5½; xi + 372; 1942.

Several sections of this edition have been altered or rewritten since the previous issue (noticed in Q. R. B., Vol. 11, p. 108) appeared. As before, the treatment is essentially comparative, with amphioxus, frog, chicks and man considered at comparable stages of early development. Organogeny is taken up by systems, with frog, chick, and human material treated separately. All sections are well illustrated, particular use being made of diagrammatic representations. With a view to making it more valuable to premedical students, the space devoted to human embryology has been considerably increased over previous editions. This addition has not lengthened the book as the sections dealing with laboratory material have been shortened. The chapters on the anatomy of vertebrate embryos in the third edition have been reduced to an atlas of illustrations of typical specimens and sections from the frog, chick, and 10 mm. pig, and the section on technique has been reduced to a single chapter.

The book contains one chapter which deals somewhat superficially with the problems of experimental embryology, but there appears to have been little effort to correlate this with the descriptive material presented.

Some sections of the book give rather thorough and up-to-date accounts of specific phases of development. However, one gets the impression, particularly in some sections on organogeny, that an effort has been made to present too many different things in too little space. This has frequently made it necessary merely to state that a structure appears at a certain time, rather than to give details of its formation. Specific references to similarities and differences which might be expected in a comparative work are limited for the same reason.

The book contains a glossary, index, and a limited bibliography (mostly of books) classified under several headings.



EMBRYOLOGY OF THE RHESUS MONKEY (MACACA MULATTA). Collected papers from the Contributions to Embryology, published by the Carnegie Institution of Washington. Publication 538.

Carnegie Institution of Washington, D. C. \$1.00. 11½ x 9; 66 + 48 plates; 1941 (paper).

In the present volume the following five important papers on the placentation and early development of the Rhesus monkey are conveniently brought together and reissued for the use of investigators in the field of primate embryology: (1) First maturation division of the Macaque ovum, by Carl G. Hartman and George W. Corner; (2) Tubal ova of the Rhesus monkey, by Warren H. Lewis and Carl G. Hartman; (3) Development of the Macaque embryo, by Chester H. Heuser and George L. Streeter; (4) Fetal growth and develop-

ment of the Rhesus monkey, by Adolph H. Schultz; and (5) Placentation of the Macaque, by George B. Wislocki and George L. Streeter.

The first three are recent publications (see Q. R. B., Vol. 17, p. 181 for a review of these articles). The last two were published in 1937 and 1938 respectively (see Q. R. B., Vol. 14, p. 254 for a review of the Wislocki-Streeter paper). A full reference to each of the original articles is given in the table of contents.

During the years in which the attention of the Carnegie Embryological Laboratory has been devoted primarily to the development of the Rhesus monkey, tremendous progress has been made in the advancement of knowledge concerning early primate development. Their valuable Macaque collection represents an abundance of material of known conception age, collected and studied with superior facilities. While the use of the same material by different authors has resulted in some overlapping, it will be found that the papers supplement each other, and, taken as a whole, cover the principal developmental and growth phenomena that characterize this important animal.



TEXTBOOK OF EMBRYOLOGY. *Fourth Edition.*

By Harvey Ernest Jordan and James Ernest Kindred. D. Appleton-Century Company, New York and London. \$6.75. 9½ x 6½; xiv + 613; 1942.

The merited success of this useful and straightforward account of human development has resulted in a new, fourth edition.

While the present volume is constructed upon the same basis as its predecessors, the addition of important new descriptive material has made necessary a considerable amount of revision. Some chapters have been rearranged to give a more logical sequence and some of the earlier shorter chapters have been placed as sections, in small type, under the proper large chapters.

Perhaps the most valuable new feature is the addition of the more significant recent experimental and comparative data distributed among the respective chapters for the most part as separate terminal sections. This new material includes recent investigations on inducers, hormones, vitamins, parthenogenetic agents, *in vitro* development of mammalian embryos, and the results of various transplantation and extirpation experiments. References to the literature are placed as footnotes and collected in an alphabetically arranged bibliography at the end of the book.

The illustrations are well chosen and abundant. Many of the earlier figures have been eliminated and many new ones added.

ANATOMY OF THE NERVOUS SYSTEM: A Textbook from the Developmental and Functional Point of View, and Atlas of the Nervous System of Man.

By Olof Larsell. D. Appleton-Century Company, New York and London. \$6.50. 9½ x 6½; xviii + 443; 1942.

Although intended primarily as a medical text this book will prove a valuable addition to the general biological reference library. It presents not only a comprehensive account of the fine anatomy of the human nervous system but also a fairly complete consideration of its histogenesis and physiology. Each major division of the nervous system is treated in an individual chapter and brief summaries of illustrative lessons are given at the end of many of the chapters. Many excellent illustrations of sections and interpretive diagrams are included in the text and a special-series of figures of sections of the central nervous system is arranged in atlas form at the end of the book. The book is authoritative, modern in outlook, logical in treatment, and extremely well written. There is a good bibliography and a full index.



MAMMALIAN STRUCTURE: *Atlas and Laboratory Manual of Cat Anatomy.*

By Charles J. Wideman, S. J. Loyola University Press, Chicago. \$1.20. 11 x 9½; 60; 1941 (paper).

Designed for a one semester course in cat anatomy, this manual contains instructions for dissection and is illustrated with 34 original figures. The treatment is logical and the directions are easily followed. This reviewer feels, however, that there are several omissions which could hardly be justified in a course devoted exclusively to mammalian anatomy. The most serious of these is the lack of any mention of the autonomic nervous system. There is also no consideration of the external features of the body, the integumentary musculature is not mentioned, and the description of the body musculature is confined to the most superficial muscles of the lateral surface of the body, arm and leg. The last 19 pages of the manual are devoted to a full pronouncing glossary and an index.



PHYSIOLOGY AND PATHOLOGY

ANOXIA: *Its Effect on the Body.*

By Edward J. Van Liere. The University of Chicago Press, Chicago. \$3.00. 9 x 6; xiii + 269; 1942.

This survey covers very thoroughly the work done on oxygen want, particularly the important developments within the last 25 years. The earliest studies on oxygen were reported by Lavoisier in 1777 in his paper "Experiments on the respiration of animals and the changes

which the air undergoes in passing through the lungs." It was not until nearly a century later (1875) that the French physiologist, Paul Bert, becoming interested in newspaper accounts of the effect of rarefied air on those who ascended to great heights in balloons, began the serious study of the effect of variations of barometric pressure on man. He persuaded three scientists to make an ascension for observational purposes. Although provided with oxygen, all three became too weak to make use of this. Two of the men died. The third became unconscious but lived, although, according to the instrument, the balloon reached a height of 28,200 feet. Since that time much work has been done on anoxia, especially since the greatly increased use of airplanes in recent times.

Four types of anoxia are recognized: (1) anoxemia, the most serious form, where there is lack of oxygen in the arterial blood. This type is characteristic at high altitudes, although it is produced by any condition which prohibits oxygen passing into the blood, such as in pneumonia, drowning, shallow respiratory movements, and embryological malformations of the heart or blood vessels; (2) anemic anoxia, where there is oxygen in the arterial blood but a shortage of functioning hemoglobin; (3) stagnant anoxia, where the arterial blood has a normal amount of oxygen but it is not given off to the tissues in sufficient quantities; (4) histotoxic anoxia, where the tissue cells are poisoned and unable to properly use the oxygen. All of these forms of anoxia have a profound effect on the body. Since they can be artificially induced it is possible to study them by the experimental method, either on man or animals. Following a discussion of these various laboratory procedures the author takes up the effect of anoxia on the various organs of the body: blood pressure, respiration, lymph, secretion of urine, metabolism, heat regulation, nutrition, water distribution in the body, and the nervous system. Of particular interest to the general reader at the present time are the chapters dealing with respiration, mountain sickness and high altitude sickness, acclimatization, and the nervous system.

Van Liere states that:

... nervous tissue is the least capable of withstanding oxygen want. Whereas cartilage tissue, for example, may withstand total deprivation of oxygen for several hours without suffering any apparent deleterious effects, nervous tissue can withstand deprivation of oxygen for only a few minutes.

From the practical standpoint of the effect of anoxia on the special senses, the effect on the eye is doubtless the most important. There is evidence that there is a loss of accommodation and loss of visual acuity at altitudes at which pilots fly. There is also evidence that there may be some persistent aftereffects if the pilot has subjected himself to extreme altitudes. It is obvious that these aftereffects could well cause trouble in flying at lower levels and also in landing. Nearly all observers agree that the organ of hearing is the most

resistant of all to anoxia, and, for practical purposes, it probably functions until psychomotor collapse occurs.

The volume contains tables and figures (17) in the text, each section is thoroughly documented and an excellent working index is provided.



HIPPOCRATIC MEDICINE: *Its Spirit and Method.*

By William Arthur Heidel. Columbia University Press, New York. \$2.00. 8 x 5½; xv + 149; 1941.

Concerning Hippocrates very little is known with certainty. Although his contemporaries are agreed that, unlike Socrates, he did commit his theories and teachings to writing, there are no existing documents that can be considered accurate copies of what he may have written. Yet there is a great body of anonymous medical treatises dating from the age of Hippocrates and later times, some of which undoubtedly embody his beliefs, but there is so much inconsistency among them that it is hardly possible to put one's finger on any specific statement and say "This is authentic" or to say of another "This is an interpolation."

But if we broaden the term "Hippocratic medicine" to make it include all the body of medical belief that had accrued in Greece during the fifth and fourth centuries B.C. and make this the subject of inquiry, the fact stands out that at this time medical thought was divided up into rival schools of conflicting opinion just as it is today. Conspicuous among these was that at Cos to which Hippocrates himself belonged, and the rival school of Cnidos. But it is not known what specific medical theories characterized these schools. For instance, in one ancient document we find quoted the commonplace proverb, "One man's meat is another man's poison," while in another it is naively stated that every symptom has its own specific remedy with which it should invariably be treated, and since all the remedies are known it is impossible that any advance in medical theory can ever take place. There was also much argument as to whether medicine was an art, a science, or a philosophy. Whatever Hippocrates may have thought about what medicine was, there is no doubt at all as to what he thought it ought to be. The entire object of his writings was to make medicine scientific.

It was for this reason that Hippocrates has been called the "Father of Medicine." He was not the first physician in history—far from it. The first Greek philosopher of whom we have any record, Anaximander, was also a physician, and there is evidence in the Homeric epics of medical activity in those days. But Hippocrates was the first to attempt to put medicine on a strictly scientific basis, and to appreciate what this involved we must know something about Greek sci-

entific method. A whole chapter is devoted to this subject.

It was Heidel's intention to write a series of books, covering all phases of Greek science, of which the present work was to be one. But unfortunately death intervened just after the first volume was completed. While we cannot but regret that the author was not spared to complete his labors we can at least be grateful that this one treatise has appeared.

The index covers nine pages and appears to be quite detailed.



IMMUNOLOGY. *Second Edition.*

By Noble Pierce Sherwood. C. V. Mosby Company, St. Louis. \$6.50. 9 x 5½; 639; 1941.

The author indicates in the preface that this book is primarily written for medical students. It seems well adapted for this purpose especially during the present national emergency when the medical curriculum is accelerated and the conservation of time is so important. The author has refrained from entering into lengthy discussions of debatable points, but has presented the existing opinions of the authorities in clear, concise statements. Due to the many subdivisions of the chapters and the frequent definitions of terms, the reading of the subject matter is not always smooth. In fact one may occasionally feel as though he is reading a dictionary or a pocket encyclopedia. However, these properties together with a style of writing that is easily understood make the book a good text for its designed purpose.

The theoretical background of immunological reactions is presented in such a manner that the student will be better able to evaluate properly the significance of diagnostic tests as performed in the laboratory. Many of the diagnostic tests in widespread use are described in sufficient detail to be understood, but not adequately enough to serve as a laboratory guide. References are given at the end of the chapters for those who wish to consult the original literature or desire full descriptions of the laboratory technique.

Two worthwhile chapters have been added to the second edition of this book, one on the reticulo-endothelial system and the other on serum reactions. For those not acquainted with colloidal chemistry an elementary discussion of the subject is presented in the appendix. Many black and white figures and several colored plates illustrate the text. Author and subject indexes are included.



NEURAL MECHANISMS IN POLIOMYELITIS.

By Howard A. Howe and David Bodian. The Commonwealth Fund, New York; Oxford University Press, London. \$3.00. 10 x 6½; vii + 234; 1942.

At the present time, investigators in the field of poliomyelitis are not so pessimistic as they were a few years ago. Indeed, there is an optimism in the group that presages intensive and fruitful work in the near future. However, one is struck by the lack of investigators in this field who have had fundamental training in neuroanatomy or neurology. Progress is being made, however, and already there are some neurobiologists who have been making significant contributions to the subject of poliomyelitis, as is evidenced by the present book. This excellent monograph, in which are recorded the investigations of two workers, embodies a series of experiments, many of them already published, which grew out of the problem concerning the rôle which nerve fibers and nerve cells play in the penetration into and migration of the virus within the body. In presenting this material, the authors have attempted not only to achieve a broad and unified basis for further investigations of virus-neuron relations in general, but also to include some of the possibilities which such a study offers for understanding both the behavior of the virus and the biological processes in the nervous system. Material presented includes: the mechanism and rate of virus spread in peripheral nerve, the genesis of cerebral lesions, the rôle of neurons in the dissemination of virus in the central nervous system, the behavior of virus in peripheral nerves and in non-nervous tissues, the portal of entry problem in man and in experimental animals, the pathology of early arrested and non-paralytic poliomyelitis, virus-refractory states in nerve cells, and problems of immunity in poliomyelitis presented by second attacks. The book is effectively illustrated with microphotographs, charts and tabular material and is provided with an extensive bibliography and a complete index.



ENCEPHALITIS. *A Clinical Study.*

By Josephine B. Neal and Collaborators. Grune and Stratton, New York. \$6.75. 9 x 6; xviii + 564; 1942. This book adequately fulfills a long-felt demand of the medical profession for an easily available source of information pertaining to the various encephalitides and to the clinical treatment of these dread maladies. Josephine Neal and her equally qualified collaborators have done a remarkable job of organizing and presenting the present knowledge of these diseases, of which a great amount must be accredited to them and their exhaustive research program.

The first chapter, by Neal, deals with a general discussion of encephalitis regarding the etiologic agents involved, viral and otherwise, and the great difficulty of making differential diagnoses clinically. R. S. Muck-infuss presents in the second chapter an excellent report on the epidemiology of epidemic encephalitis. The following headings of the remaining chapters indicate the

character and scope of the book: Neurological complications following acute infections and vaccination; The clinical course of epidemic encephalitis; The treatment of epidemic encephalitis; The surgical treatment of post-encephalitis; Post-encephalitic behavior disorders in childhood; The pathology of encephalitis.

The chapters on the clinical course of epidemic encephalitis and pathology of encephalitis are particularly well integrated and complete with case histories and necropsy reports. The chapter on the treatment of epidemic encephalitis is interesting and instructive. Vaccines, such as herpes vaccines, and drugs, such as bellabulgar, that show promise therapeutically are discussed.

Each chapter has an extensive bibliography. The book has an adequate subject index as well as a useful index of proper names.



FOUR TREATISES OF THEOPHRASTUS VON HOHENHEIM CALLED PARACELSUS.

Edited, with a Preface by Henry E. Sigerist. Translated from the Original German, with Introductory Essays by C. Lilian Temkin, George Rosen, Gregory Zilboorg and Henry Sigerist. The Johns Hopkins Press, Baltimore. \$3.00. 9 x 6; xii + 256; 1941.

Published in commemoration of the four hundredth anniversary of the death of Paracelsus, this book presents translations of four of his treatises, chosen to illustrate four different aspects of his work. The first treatise, the *Sieben Defensiones*, is Paracelsus' own justification of his ideas and methods; the second, an essay on the diseases of miners, is the first monograph ever written on the diseases of an occupational group; the third, concerning mental diseases, is a pioneering work in psychiatry; the fourth, a treatise on nymphs, sylphs, pygmies, salamanders and other spirits, is included as a sample of the philosophy and theology of Paracelsus.

The importance of Paracelsus in the history of medicine has long been a controversial point among historians. His erratic ways and his violent tirades against contemporary physicians gave rise to much bitter criticism of him and his methods, which could not fail to influence the opinions of later writers. A first-hand evaluation of Paracelsus' thoughts through study of his works has been impossible for the average reader because his books were all written in the 16th century German of Switzerland, a language which offers peculiar difficulties to the translator. The present translations, together with the brief but illuminating introductory essays which accompany them, give the reader a basis for forming a real considered judgment concerning the place of this almost legendary figure in the development of science. We predict that an increased recognition of the originality and sincerity of the man and a lessen-

ing of emphasis on the "bombastic" phase of his character, will result.



A MANUAL OF ENDOCRINE THERAPY.

By Bernard L. Cinberg. Chemical Publishing Company, Brooklyn. \$3.25. 8½ x 5½; v + 178; 1942.

The field of endocrinology has expanded so rapidly during the past decade that the general practitioner cannot even hope to keep abreast of the subject. Even if he had time to read all the literature, there would still remain for him the colossal task of critically analyzing and evaluating the various new therapeutic agents, procedures and practices in order to decide what is practical and what is impractical in meeting his own clinical problems.

In this little book, Cinberg has attempted to bring together the pertinent aspects of modern endocrinology and arrive at a safe and sane plan of endocrine therapy for the general practitioner. The result is not a textbook, hence it presents the subject without the details, the controversies and the lengthy bibliographies that burden modern endocrinology literature. The discussions are centered around a number of commercial endocrine products, and are concerned with their therapeutic value in treating human maladies. Where observations on the human have not confirmed the findings on certain lower mammals, the author states the facts quite frankly, and warns against the dangers patent in the assumption that what will work with a rat will work with a human.

The short section on diagnostic procedures in endocrine malfunction designed for the unassisted practitioner, and the list of therapeutic suggestions for treating a variety of maladies relating to the endocrines, contribute alike to the excellence and usefulness of this volume in the hands of the hurried and harried physician.



LABORATORY DIAGNOSIS OF PROTOZOAN DISEASES.

By Charles Franklin Craig. Lea and Febiger, Philadelphia. \$4.50. 9¼ x 5½; 349 + 4 plates; 1942.

This excellent book is intended as a guide to diagnosis of protozoan diseases particularly for the less expert physician and laboratory technician. As such it serves its purpose admirably. The sections on each disease contain detailed descriptions of the morphology of the parasite, methods of collection and microscopic examination, methods of culture, serological tests for the presence of the parasite, and a general critique of the various diagnostic procedures. The different methods are described in great detail, and the precautions necessary for their successful use are pointed out. The diagnostic worth of each method is critically evaluated,

in many cases on the basis of the author's own experience. Of particular value are the suggestions made as to diagnostic procedures to be used by laboratories of limited facilities. The book is well and amply illustrated with drawings and photographs of all the organisms mentioned. Considerable care was used to show the various forms which each organism may take.

The book is divided into six parts. The first deals with amebiasis and flagellate infections; the second with the leishmaniasis; the third with the trypanosomiasis; the fourth with coccidiosis; the fifth with the malaria plasmodia; and the last with balantidiasis. There is an extensive list of references and both an author and a subject index.



BAINBRIDGE AND MENZIES' ESSENTIALS OF PHYSIOLOGY. *Ninth Edition.*

Edited and Revised by H. Hartridge. Longmans, Green and Company, New York and London. \$5.00. 8½ x 5½; x + 687; 1941.

The original purpose of this book (cf. Q. R. B., Vol. V, p. 253 for mention of an earlier edition) was to provide, in concise form, the fundamental facts and principles of physiology and thus to serve as an aid to medical students preparing for examinations in physiology. The book well accomplishes this purpose inasmuch as it contains the essentials of mammalian physiology.

In the eighth edition, many chapters were rewritten and the whole book was brought up-to-date. As a consequence there was no complete rewriting of chapters for the ninth edition. In many cases, however, new material has been substituted for the old in such a way as to retain the size of the book as a whole. Although relatively complete on such subjects as the circulatory system, muscle and nerve physiology, the book is not detailed in its treatment of metabolism, vitamins, etc. While no bibliography is included this is hardly essential considering the purpose for which the book is designed. The excellently prepared index will be found most useful to students.



ALIMENTACION Y NUTRICION EN COLOMBIA

By Jorge Bejarano. Editorial Cromos, Bogotá. 8 x 5½; 166; 1941 (paper).

The author, professor of hygiene at the University of Bogotá and president of the Red Cross of Colombia, from the evidence presented in this book appears to be greatly distressed over the lack of good judgment in the choice of foods by a large percentage of the population of his country. He finds that they use too much sugar and starchy food and too little meat, milk, eggs, fruits and vegetables. Likewise the consumption of locally-made alcoholic drinks is excessive. He states, how-

ever, that in most places water supplies are poorly guarded and sometimes become contaminated with fecal material. Under these circumstances especially we should be inclined to agree with the natives that water is indeed unfit to drink and alcohol a beverage to be preferred. The book contains a good account of the recent advances in the science of nutrition. It should be of interest and profit to physicians, public health workers, and intelligent laymen in Colombia and among other Spanish-speaking populations.



BIOCHEMISTRY

BIOLOGICAL SYMPOSIA, Volume V. *I. Comparative Biochemistry. II. Intermediate Metabolism of Fats. III. Carbohydrate Metabolism. IV. Biochemistry of Choline.*

Series Edited by Jaques Cattell. Volume V Edited by Howard B. Lewis. Jaques Cattell Press, Lancaster, Pennsylvania. \$3.00. 9½ x 6½; ix + 247; 1941.

This fifth number of the series published by the Jaques Cattell Press is the second dealing with current biochemical problems. This volume is composed of the four symposia arranged by the Council of the American Society of Biological Chemists for the Chicago meeting of the Federation of American Societies for Experimental Biology in April, 1941. The first section consists of papers on End products of nitrogen metabolism in plants and animals, by H. B. Vichey and H. B. Lewis, and on The merging of growth factors and vitamins, by W. H. Peterson. These papers, presented with the purpose of directing the interests of some of the young students of biology to the significance and importance of the study of comparative biochemistry, make profitable reading and should go far toward accomplishing their end.

Aspects of the intermediary metabolism of fats are treated by H. E. Carter, S. Soskin and R. Levene, R. G. Sinclair, and H. E. Longnecker. In the symposium on Carbohydrate metabolism, problems of oxidation, phosphorylation, etc. are discussed by T. R. Hogness, C. F. Cori, O. Meyerhof, and E. A. Evers, Jr. These two sets of articles emphasize the close interrelationships existing between fats and carbohydrates in their utilization by the organism. Both stress the importance of phosphoric acid as an intermediary agent in both fat and carbohydrate metabolism. Oxidation of fatty acids is presented in direct relationship to that of carbohydrates.

In the fourth section, The biochemistry of choline, E. W. McHenry, W. H. Griffith and D. Glick respectively consider the relations of choline to fat metabolism, to pathological changes in the liver and kidneys and to functions of the nervous system. The rôle of choline in the important process of transmethylation and its relation to methionine and creatine formation

are ably discussed by V. du Vigneaud in the concluding paper.

Because this volume deals with some of the newest and most revolutionary aspects of modern biochemistry, it must perforce make fascinating reading to most biologists. One might class these papers as progress reports. In most instances the authors have presented the facts of the subject in a logical and interesting manner and with a minimum of theorizing beyond the data. To some this will indeed be refreshing; unfortunately it is not always a characteristic of general review papers. The volume should find a wide audience not only among biochemists, but also among biologists in general.



THIS CHEMICAL AGE: *The Miracle of Man-Made Materials.*

By Williams Haynes. Alfred A. Knopf, New York. \$3.50. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; vii + 385 + xxii. 1942.

Discoveries made since World War I by American workers in the field of synthetic chemistry have been numerous and almost miraculous. The author's purpose in writing this book is to give, in non-technical language, a clear picture of the origin and growth of our great modern chemical industry and to bring out the effect which it has had in the life of each one of us.

The first two chapters are devoted to an explanation of the few basic chemical facts necessary to an understanding of what is to follow. Then, in order, are discussed coal tar dyes, perfumes, pharmaceuticals, sulfa drugs, rubber, textiles, plastics, and munitions. The author shows how World War I, by cutting off our supply of synthetic chemicals from Germany, was of prime importance in making the present day American chemical industry foremost in discovering and producing synthetics in the world. Emphasis is placed on the fact that man-made copies of natural products are not mere substitutes but are usually superior to the natural products.

The book is, in general, well written and is easy to read. There are a few technical errors which might be ascribed to the proofreader. The book will not interest the trained chemist. However, it should appeal to the general reader and hence it fulfils its purpose.

A brief annotated list of additional titles of a general chemical nature, a glossary of terms, and a very good index are included.



SYNOPSIS OF APPLIED PATHOLOGICAL CHEMISTRY.

By Jerome E. Andes and A. G. Eaton. C. V. Mosby Company, St. Louis. \$4.00. 7 $\frac{1}{2}$ x 4 $\frac{1}{2}$; 428; 1941.

Although this book was written as a text, the authors point out in the preface that "in some ways the book may be regarded more as a handbook than as a text."

This is undoubtedly true as most of the book is primarily a catalogue of short statements of chemical changes accompanying various physiological and pathological conditions, and equally short statements of testing methods.

By far the largest part of the book is devoted to the blood, with shorter sections on the cerebrospinal fluid, urine, functional tests, gastric analysis, and basal metabolism. Most of the tests commonly applied are given, and references to tests for constituents not discussed are given in several places. There is no discussion of tissue analysis. The laboratory methods are not extensively discussed from a biochemical standpoint, but the "cook-book" directions and the provision of formulae for calculating quantitative results should appeal to those who have only occasional recourse to biochemical tests. References are given for many, but not all of the tests. There is a complete index and an appendix with instructions for the preparation of reagents and standard solutions.

This volume is primarily for the physician and medical student rather than for the biochemist, and should prove a valuable book in its field.



VITAMINS AND MINERALS FOR EVERYONE.

By Alida Frances Pattee. Hazel E. Munsell, Technical Advisor. G. P. Putnam's Sons, New York. \$2.00. 8 x 5 $\frac{1}{2}$; xviii + 242; 1942.

In this book the latest findings on vitamins and minerals are rather interestingly arranged for quick reference. The material has been extremely simplified so that no specialized knowledge is required to understand it. At a glance one is told what the various vitamins and minerals are, what they do for the body, what foods contain them, and how much of these foods one needs daily.

One valuable and useful feature is the presentation of Food Tables from which the vitamin and mineral adequacy of a diet can be determined without the usual calculations. These tables show how much of each vitamin and mineral may be obtained from average servings of many of the most common foods. Other tables show foods in the order of their descending potency from those containing most to those containing least of these substances.

Vitamin concentrates are discussed, and sample menus are suggested which furnish a day's quota of vitamins, minerals, and calories for a sedentary adult.



SEX

OUR SEX LIFE. *A Guide and Counsellor for Everyone. Second Edition, Revised.*

By Frits Kahn. Translated from the German by George Rosen. Alfred A. Knopf, New York. \$5.75. 9½ x 6½; xxxv + 459 + 41 plates; 1942.

This second edition of *Our Sex Life* (cf. Q. R. B.: 1939, 3, p. 377 for notice of the earlier edition) is not significantly different from the first. Kahn presents a thorough and interestingly written discussion of most phases of sex anatomy, sex hygiene, sex behavior, and the numerous sex problems facing the individual. "Although the author at times waxes a little too poetic, the book contains more sense and fundamental information than many of the *vade mecum*s of the sex life now on the market." It is to be noted that the book still contains a striking contradiction to the later experimental work: "There are no 'safe' days during the woman's monthly cycle." The "numerous theories concerning allegedly 'safe' periods . . . are pure creations of fantasy."

As a whole, however, this translation of *Unser Geschlechtsleben* is excellent and deserves a high rank among books of its type.



BIOMETRY

PHYSICAL MEASUREMENT OF YOUNG CHILDREN: *A Study of Anthropometric Reliabilities for Children Three to Six Years of Age. University of Iowa Studies. Studies in Child Welfare. Volume XVIII, Number 3. Serial Number 394.*

By Virginia Bergstresser Knott. University of Iowa Press, Iowa City, Iowa. \$1.35 (cloth); \$1.00 (paper). 9½ x 5½; 99; 1941.

Variation in physical measurements resulting from differences in technique is a constant challenge to the anthropometrist who strives for some measure of reliability in his work. The present study was undertaken for the primary purpose of evaluating the differences arising from three different sources, namely: (1) those resulting from observations by two different technicians; (2) those arising from successive observations of the same measurement by a single technician; and (3) those arising from the observations of a single technician on a subject being measured from several positions. A secondary aim of the study was that of determining the most reliable methods for measuring pre-school children.

Thirty-five different physical measurements on some 131 different children ranging in age from 3 to 6 years make up the data herein presented. In general, it was found that successive independent observations by a single technician showed less variability than those between two different technicians. No marked differences were found in reliability of measurements taken with the subject in two different positions. For a complete record of growth in pre-school children, the author

recommends that stature be measured at least 10 times a year; length of extremities and body girths, 3 or 4 times a year; and extremity girths and head measurements about once or twice a year.

The report includes a critical evaluation of 44 papers on anthropometry, and a number of tables, graphs and photographs.



STATISTICAL METHODS APPLIED TO AGRICULTURAL ECONOMICS.

By Frank A. Pearson and Kenneth R. Bennett. John Wiley and Sons, New York; Chapman and Hall, London. \$4.00. 9 x 5½; vii + 443; 1942.

This book was written primarily for those interested in the application of statistical methods to agricultural economics. The illustrations are largely drawn from the fields of farm management, marketing, and prices. However, these illustrations are similar to those which might have been taken from other fields in agricultural economics and business, so that the usefulness of the book to the general statistician is thereby much enhanced. The volume is designed for use as a textbook in colleges and universities, or as a general reference book for statistical workers. The arrangement follows the usual procedure: measures of central tendency, variation, association and reliability. The book differs from most textbooks in that it contains two chapters on the tabular analysis of relationships—a subject ignored in many texts. In the chapters on testing reliability, emphasis is placed on problems which arise in the social sciences. The appendix contains: A Glossary of symbols used in the book, A method of calculating sums of squares and sums of products with tabulating equipment, The Doolittle method of solving normal equations for net regression coefficients, and other general tabular information. References are given as footnotes in each chapter. An index has been provided. This volume makes a significant contribution to literature in the statistical field, and should serve as a useful tool for research workers, students and teachers alike.



THE BULLETIN OF MATHEMATICAL BIOPHYSICS. Volume 4, Number 3, September, 1942.

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: A mathematical theory of protoplasmic protrusions: I, by Henry E. Stanton; A theory of electrical polarity in cells: II, by Robert R. Williamson; Green's functions in biological potential problems, by Alvin M. Weinberg; Further contributions to the mathematical biophysics

of visual aesthetics, by N. Rashevsky; Some observations on the simple neuron circuit, by Walter Pitts; Delayed absorption and diffusion in colloidal media, by Herman Branson; An expression for the rate of return of an egg after artificial deformation, by H. D. Landahl.



PSYCHOLOGY AND BEHAVIOR

FOUNDATIONS FOR A SCIENCE OF PERSONALITY.

By Andras Angyal. *The Commonwealth Fund, New York.* \$2.25. 8½ x 5½; xii + 398; 1942.

In this book the author has attempted to outline a general theoretical basis for a "science of personality," holistically conceived. He starts with the premise that such a basic theory must fulfill three conditions. First, it would require more specific and positive formulations with regard to the nature, organization and laws of personality, than are at present available. Under this heading the general pattern of life processes is considered in its dual nature—the tendency toward increased autonomy (self-determination, mastery of environment, aggression or regression) and the tendency toward homogeneity (the trend of the individual to conform with the superindividual wholes of society, culture, etc.). The second desideratum would be the formulation of a method of synthesis of segmental data whereby the facts of anthropology, psychology, physiology, biology and other "segmental sciences" would be related not with each other but rather to the "psychophysically neutral processes" of the total organisms. In this connection the author elaborates a theory of "systems" which may be summarized as follows: "Parts are characterized by being relatively complete in themselves and by occupying a position directly in a system. The concept of part should be restricted to mean 'immediate' part. System action spreads in a continuous manner upward or downward over the entire whole or it may be limited to a certain region." The third condition is stated as the development of a new set of concepts of terms, in general more dynamic than those employed in the "segmental" sciences. However, the author suggests very few new ones but does assign new meanings to a number of current and generally accepted terms.

The greater part of the book was presented in a series of lectures at the Henry Phipps Psychiatric Clinic of the Johns Hopkins University. Its interest is not restricted, however, either in its general import or in the specific problems of illustrations advanced, to the psychiatric field. It is a stimulating, well-written book, offering an interpretative background for empirical findings that should be of interest to anthropologists, biologists, physiologists, psychologists and others.

A LONG-TERM STUDY OF THE EXPERIMENTAL NEUROSIS IN THE SHEEP AND DOG with Nine Case Histories. *Psychosomatic Medicine Monographs, Volume II, Nos. III and IV, 1941.*

By O. D. Anderson and Richard Parmenter. *National Research Council, Washington, D. C.* \$3.50. 10 x 6½; vii + 147; 1941.

In this report of a long-term investigation of neurosis in the sheep and dog, carried on at the Cornell University Behavior Farm, in Ithaca, N. Y., the authors have presented in detail their methods of procedure and their observations. Their approach is that of the conditioned reflex method. Their primary interest is in the causative factors at the basis of the neurotic disorders induced. The second chapter is devoted to a detailed description of the manifestations of experimental neurosis, and the wide variation in symptomatology is stressed. In the third chapter, procedures which precipitate and maintain the neuroses are described. Particularly interesting are the comments on the influence of the examiner on the experimental animals' reactions.

A discussion of the experimental findings is presented in the fourth chapter. As a working hypothesis, the authors state: "Repeated and prolonged emotions, incident to the experimental procedure, produce a chronic imbalance of the internal secretions which induce a constant state of imbalance of the chemistry of the nerve cells. A change in the irritability of the nervous system results. The nervous system may become hyperirritable." The authors feel that by laying a groundwork of physiological findings they will have a basis for later more extensive psychological investigations of neurosis.

In the Appendix, a case history of each experimental animal is presented. There is a bibliography of 24 titles.



THE MEASUREMENT OF ADULT INTELLIGENCE. *Second Edition.*

By David Wechsler. *Williams and Wilkins Company, Baltimore.* \$3.50. 9 x 6; xi + 248; 1941.

This second edition of Wechsler's book (first edition noticed in Q. R. B. Vol. 15, p. 117) follows closely the first edition. The development and use of the Wechsler-Bellevue Scales are described in detail. The material is presented in three parts. Part I is devoted to an excellent discussion of the nature and classification of intelligence. In Part II, the Bellevue Scales are considered in detail. In the present edition, a new chapter, Diagnostic and clinical features, is included. Part III consists of the manual of instructions in the criteria for scoring the various tests. There are five short appendices of special statistical methods used. A final section is devoted to intelligence quotient tables. There is an index.

YOUR PERSONALITY: *Introvert or Extrovert?*

By Virginia Case. The Macmillan Company, New York. \$2.50. 8½ x 5½; viii + 277; 1941.

This book which is written in popular style and for popular consumption, presents the concepts of the Swiss psychiatrist Carl Gustav Jung, encompassed by the terms "introvert" and "extrovert," in relation to types of temperament. The manuscript was read by Jung and approved by him for publication. The author offers no original ideas of her own, but her presentation of Jung's concepts seems accurate and clear. The book has little technical interest, but is readable and will no doubt find its public among those whose reading is motivated by a desire for self-understanding and self-help.

**PHYSIOLOGICAL PSYCHOLOGY.**

By S. R. Hathaway. D. Appleton-Century Company, New York. \$2.75. 8 x 5½; xxi + 335; 1942.

This book is designed as a text to acquaint the psychologist with basic facts relating to the anatomy and physiology of the human nervous system. The subject matter, in the main, is descriptive and presents a concise summary of current knowledge of the structure and function of nervous tissue. There is little of actual "psychology" included, and the viewpoint is essentially mechanistic. There is a selected bibliography and an index.



**DE OMNIBUS REBUS
ET QUIBUSDEM ALIIS**

A SHORT HISTORY OF SCIENCE to the Nineteenth Century.

By Charles Singer. Clarendon Press, Oxford; Oxford University Press, New York. \$3.75. 8½ x 5½; xiv + 399; 1941.

Doctor Singer begins his interesting history with the definition of science. This he conceives to be "no static body of knowledge but rather an *active process* that can be followed through the ages." Science was an active process when early man was learning and improving methods of producing fire. The beautifully drawn cave pictures of the bison with arrows embedded in the heart (a pictorial study of the method of killing) are evidences of accurate observation and a knowledge of anatomy by prehistoric man. In the agricultural stage, man developed a system for determining the onset of the season which led to a calendar. With commerce, the system of numerical notation evolved. Of the "great primary discoveries which made social life possible" nothing is known. Nevertheless the people who made these discoveries were taking part in the development of science. They were doing the spade-work which made it possible for later civilizations to produce men "who

were conscious of science as a distinct process and who were conscious, too, that the process might be indefinitely extended. . . ." While the present work begins with the earliest known records that are in any degree complete, the author believes that ultimately a work will be written that will include many of the sources of scientific development of the ancient world. "The ancient world presents us numerous such instances fathered by necessity and mothered by experience. All have a like claim to be included in a history of science."

Throughout his book Singer links the progress of science with the lives of the great men in science—covering a period of about 2500 years. The first period he terms "The Rise of Mental Coherence" (600–400) and begins with the Ionian Greek Thales (629–565 B.C.). Such men as Anaximander, Hecataeus, Heracleitus, Democritus, Herodotus, Pythagoras, and Hippocrates belong in this period which culminates in the great intellectual revolution associated with Socrates (470–399). "Out of the conflict between the Socratics and the physical philosophers arose the main streams of later Greek thought. These two streams derive their titles and their tendencies from the two gigantic figures that occupy the stage during the fourth century, the age of Plato and Aristotle."

The second period (400–300) Singer terms "The Great Adventure" and here he discusses the several "unitary systems of thought" of the Platonian and Aristotelian schools. Singer has so admirably summed up in the final paragraph of this chapter the contents of the next three chapters that we quote in full, not only to give the reader a comprehension of the ground covered but an example of the author's lucid style.

In leaving the heroic age of Greek science we would again emphasize the "universal" character of the philosophical attempt that we call the "Great Adventure." The scientific activity of the age partook of the nature of what we should now term "philosophy." The object of each investigator was to fit his observations and the laws that he deduced into some general scheme of the universe. From their day to ours philosophy has continued her attempt thus to storm the bastions of heaven. But with the new age that we have to discuss, there was a failure of nerve in that great frontal attack. Science, becoming gradually alienated from philosophy, begins to proceed by her own peculiar method of limited objectives. The first series of these attempts resulted in the "Great Failure," the story of which we shall trace through two thousand years (Chs. III, IV, V). Nerve fails first, as with the Alexandrian school (Ch. III), next Inspiration falters under the Roman Empire (Ch. IV), lastly Knowledge itself fades in the Middle Ages (Ch. V). At length there is a rebirth. The science of the Renaissance—in which we still live—began again to proceed by the method of limited objectives (Ch. V). How that method differed from that with which the Great Failure is associated is a matter which we shall have to discuss.

The period 1250–1600, "The Revival of Learning," was marked by the rise of humanism, the introduction of the art of printing and the revival of the natural

sciences. It was an age of great accomplishment but the sciences were dominated by the models of antiquity. "The Insurgent Century" (1600-1700) brought the downfall of Aristotle and new attempts at synthesis. Credit belongs to Galileo more than to any other man for the break with ancient modes of thought and the opening up of new lines for scientific progress which led to The Mechanical World of the XVIII and XIX centuries, a period marked by the "Enrollment of Determinism." It is the era of Newton, Faraday, Kant, Linnaeus, Darwin, and many others who have had a profound influence on our own times.

Singer brings out very clearly that the path of scientific progress has by no means been a straight-forward line yet one finishes the book with the feeling that in the background, throughout the ages, there have been certain tendencies leading to the attained end. Many excellent drawings are included in the text. The index is confined to the names of the individuals occurring in the history.



COLLEGE AND UNIVERSITY MUSEUMS: *A Message for College and University Presidents.*

By Laurence Vail Coleman. *American Association of Museums, Washington, D. C.* \$1.25. 9 x 6; viii + 73; 1942.

The author of this work believes that every institution of learning should have not only one museum but several museums, the reason being that objects suitable for museum display are less related to each other than to the departments in which they are studied. The United States National Museum in Washington (which the author does not discuss because it is not a university museum) is an excellent example of what a university museum should not be, for here collections dealing with art, science and history are all assembled under the same roof. The student who goes to Washington for advanced research is not likely to be disturbed by the presence of objects in which he is not interested displayed in other halls of the same building, but the college student who is generally a beginner and who is also likely to be already inconvenienced by having to get his bibliographical material from a building that may occupy a position on the campus remote from the laboratory and the class room, will be even further handicapped if the material which he wishes to examine is kept in a locality different from these.

Furthermore, there are fundamental differences among the three types of museums. The historical museum is likely to be congested with objects of no particular interest donated by well meaning patrons who wish to get rid of them, and these the college must accept, to avoid risk of offending those on whom it may depend for pecuniary support. (The reviewer has in mind a well-known institution of higher learning which

had to accept from the bereaved heirs of its founder a wax model of the bacon and eggs which he left on his breakfast plate just before meeting a violent death. Such objects should of course be segregated in a room where the donor may inspect them but where students are not required to go.)

The exhibits in the art museum are for obvious reasons likely to be loans. Since these circulate through many museums it follows that in the long run the exhibits in different museums are likely to be very much the same. On the other hand, the exhibits in the museum of science are likely to be the property of the college, and if these exhibits illustrate what the Germans call *Heimatskunde* as they should, every college museum is likely to have its own personality, distinct from all the others.

The administration of such a museum presents problems quite different from those which arise in the case of the art museum and constitute another reason why the two kinds of museums should not be consolidated in the same building.

On the other hand, if each department has its own museum, there arises another danger to be guarded against. Museum supervision requires a highly specialized training. To build up a college collection, to index and classify new acquisitions, to keep the documentary records correctly filed, and above all to see that borrowed material is returned promptly to its correct place when due is no mean task, and requires the full time of a skilled curator. It is beyond the ability of the ordinary professor or his assistant.

The author discusses the various problems that arise in museum management and illustrates the way these have been met successfully at some of the best known universities by photographs and floor plans. He might have made his thesis more convincing by including some horrible examples of mismanagement by way of contrast, but it is not difficult to imagine why this was not done.

The author's object in writing the book is indicated by the subtitle. It would be a fine thing if every college president in the country would familiarize himself with the contents of this book.



SCIENTISTS FACE THE WORLD OF 1942: *Essays.*

By Karl T. Compton, Robert W. Trullinger and Vannevar Bush. *Rutgers University Press, New Brunswick, N. J.* \$1.25. 9 x 6; [80]; 1942.

THE UNIVERSITY AND THE FUTURE OF AMERICA.

Contributing Authors: Isaiah Bowman, Walter Bradford Cannon, Edwin Francis Gay, Herbert Hoover, Edwin Powell Hubble, Herbert Spencer Jennings, Charles Franklin Kettering, Ernest Orlando Lawrence, Archibald MacLeish, Robert Andrews Millikan, Lewis Mumford, William Fielding Ogburn, Roscoe Pound,

Aurelia Henry Reinhardt, Edward Lee Thorndike, and Ray Lyman Wilbur. Stanford University Press, Stanford; Oxford University Press, London. \$3.00. 9 x 6; ix + 274; 1941.

Probably no one will seriously question the assertion that the second world war will some day come to an end. Many of those who have access to the public ear are advising that until that day all plans for the reconstruction of civilization be held in abeyance all unmindful of the possibility that the civilized world as we have known it may vanish before our eyes in the conflagration, leaving nothing to reconstruct. These misguided prophets also seem to forget that a cessation of hostilities following the cry "*vae victis!*" is no more likely to lead to an enduring peace now than it did a quarter century ago, and that a reconstructed civilization can be no more than a hypothetical abstraction unless its foundation can be laid before the ultimate outcome of the war becomes a certainty.

Therefore we may be thankful that two of the leading universities of the country have seen fit to celebrate the anniversaries of their founding by holding symposia for the consideration of the future of civilization.

It is interesting to observe how characteristically the personalities of the two institutions are reflected in their respective symposia. Rutgers University was founded 175 years ago by descendants of New Amsterdam Dutchman, who had a reputation for business acumen (at least that is the way that Peter Kalm represented them). The contributions to its symposium are engineers. This term has acquired a wider designation than its original denotation of one who runs an engine, and in these pages we meet the terms "biological engineer" and "agricultural engineer." These expressions indicate those who approach the problems of biology and agriculture with the mental attitude and precision of the trained engineer. These are not the men who make great scientific discoveries, but those who apply the fruit of scientific achievement to human welfare. They are the spiritual descendants, not of Swammerdam or Faraday, but of Pasteur and Clerk-Maxwell.

On the other hand, Stanford University is young by comparison. Established only a half century, it is still largely colored by the memory of its first president, David Starr Jordan, whose presence we still seem to feel when walking through its halls or under the eucalyptus trees of its campus. Although a great humanitarian, his pursuit of Truth was not prejudiced by any motive of materialism. Those who participated in this symposium with one exception, do not seek to reform the world, but to understand it. Reformation may be desirable and necessary, but understanding must come first.

The best essay out of the fourteen which comprise this book is always that which one is reading at the last time.

LANGUAGE IN ACTION.

By S. I. Hayakawa. Harcourt, Brace and Company, New York. \$2.00. 7½ x 5; ix + 245; 1941.

The Trivium of the Middle Ages consisted of Logic, Grammar, and Rhetoric. These terms were more broadly construed in those days than at present; logic was the art of thinking, and grammar and rhetoric were the arts of self expression by means of the written and spoken word. Anyone who has successfully mastered these subjects need not fear for his education in any company today.

Psychologists have long argued over the extent to which thought might be possible without language. Sub-human animals have thoughts, but to what extent do they *know* that they think? If conscious cerebration depends on language, does it not behoove us to try to understand the theory of language? Do we not need to know something about the use of language, instead of being satisfied merely to know how to make use of it—a very different thing?

It is said that Tallyrand, on negotiating an international treaty suggested that if it did not contain an ambiguity one should be inserted. But probably such a step was unnecessary as all language, especially the language of diplomacy, is by nature ambiguous. Not only do the same words convey different meanings to men in Timbuktu and Paramaribo, but they convey to the same individual a different meaning today from what they did yesterday or will tomorrow.

The only language which remains unchanged throughout the ages is profane language. The dead languages do not acquire new meanings, but they are full of ambiguities acquired when they were vital media of expression. In fact, probably the chief cause of mortality among languages is that, having reached the saturation point for ambiguity, they can acquire no more. As long as a language is a living thing it must exhibit the chief characteristic of all living things—incessant change.

During the past few years thoughts such as these have actuated numerous authors to produce books devoted to the discussion of the meaning of verbal expression. Unfortunately these books are for the most part expressed in such philosophical jargon that they illustrate the difficulties that they are intended to elucidate. The single exception seems to be the one now under consideration. It is logically conceived and lucidly written, and when the author resorts to expressions that would be ambiguous in less skilful hands the content always indicates what is intended. It is even pleasant reading and will be found especially helpful by any one who contemplates writing a book on any subject.

CARNEGIE INSTITUTION OF WASHINGTON. *Year Book, Number 40, July 1, 1940-June 30, 1941. With Administrative Reports through December 12, 1941.*

Carnegie Institution of Washington, Washington, D. C.
\$1.50 (cloth); \$1.00 (paper). 9½ x 6½; xxxii + 346; 1941.

Vannevar Bush says, in the President's report,

"The Carnegie Institute of Washington is so constituted that it is bound to be deeply involved in that aspect of the present intense national effort which is concerned with the application of natural sciences to national defense, and it is necessary and fitting that the Institution should respond fully to the call of government in this regard. Inevitably, therefore, many of its long-range programs of research in the field of pure science have now been changed or held in abeyance."

Concerning defense activities: "In order that the combined effort may be properly integrated, the President of the United States has, by Executive Order, created the Office of Scientific Research and Development as a part of the Office for Emergency Management, and has given this Office the task of coordinating all defense research, and, through its subordinate bodies, of supplementing the research of the Army and Navy in the development of instrumentalities of warfare, and in medical research connected with defense. The President of the Institution is Director of this Office, and many staff members are members of its organization."

Reports are given as usual, in the *Year Book*, on the progress and development of the different departments (astronomy, terrestrial sciences, biological sciences, and historical research). The Department of Terrestrial Magnetism is heavily engaged in research on governmental problems. In a limited space it is not possible to summarize the activities in the biological sciences and in historical research. Many of these have been reported in these columns from time to time. But we wish to call attention to Corner's interesting review of the program of the Department of Embryology, in which he says:

The past history of this Department, looked at from one point of view, is a brilliant example of a planned campaign, systematically conducted. It is indeed remarkable how many of the items of Dr. Mall's original "Plea for an Institute of Human Embryology" have been successfully executed. On the other hand, a list of the individual investigations mentioned in the successive *Year Books* might suggest that the advance was not always direct. What has been done has at times not even been embryology under standard definitions of the term. . . . Yet the general result has been an advance in our knowledge of embryology in the strict sense.



NOTES ON THE PREPARATION OF PAPERS FOR PUBLICATION in *The Journal of Hygiene and Parasitology*.

By the Late G. H. F. Nuttall. *Cambridge University Press, London; The Macmillan Company, New York.*
\$1.15. 10½ x 7; 62; 1940.

We highly recommend this little volume as an invaluable guide for the young research worker in the preparation of biological papers for publication. The late Doctor Nuttall, founder of two journals, the *Journal of Hygiene* and *Parasitology*, set a high standard for the writing of scientific articles. During the long period that he served as editor (*Journal of Hygiene*, 1901-1937; *Parasitology*, 1908-1937) he assisted many inexperienced writers in preparing and improving their manuscripts for the press, with the twofold aim of raising the literary workmanship of scientific journals and of relieving the editor and the press of much unnecessary work.

From the large collection of notes which Nuttall left pertaining to the many phases of the preparation of papers for publication, the present editors of Nuttall's journals, G. S. Graham-Smith and D. Keilin, have compiled this volume. They have omitted many notes of a specialized nature, such as technicalities in printing and illustrating, in order to produce a brief, concise guide useful to those who are entering the field of scientific writing. A complete mastery by the young author of the basic rules which are herein given will simplify all his future writing. Furthermore, he will learn something of the editor's problems.

Certain "Golden Rules" are listed that must always be followed, and suggestions are given for (1) the composition of a paper (a) from original notes, (b) first, second, and intermediate drafts with general instructions pertaining to headings, footnotes, quotations, abbreviations, bibliography, style and wording, illustrations, etc.; (2) sending manuscripts and illustrations to the editor; proof reading, reprints; and finally (3) the history of a paper is given after it has been sent to the editor. The index is a model which those whose ambitions extend to more formal writing may well follow.

Books of this type are important for biological libraries. The low cost of the present volume, however, makes it available to most individuals.



THE DAYS OF CREATION.

By Willy Ley. *Modern Age Books, Inc., New York.*
\$2.75. 8½ x 5½; x + 275; 1941.

This book is an attempt to tell, in popular form, the story of the evolution of life on the earth beginning with the creation of the planet itself and continuing through to the present time. There are a number of things with which the specialist might find fault, as is probably inevitable in a popular book written by a non-specialist. However, the book is to be recommended in that it presents in many cases the evidence for the statements made. In a number of instances different theories are compared with an evaluation of the evidence for and against them. It approaches in this respect the technical writings of the professional scientist more closely than most popular books.

The book is not simply an attempt to chronicle the events in the history of life on the earth. It presents evolution as a dynamic process with emphasis on cause as well as on effect. The treatment of the causes of evolution includes a very much simplified and not too satisfactory version of the contributions of modern genetics to this field. In general the treatment of causative factors is not as satisfactory as the description of the events. Nevertheless it should give the lay reader the thought that evolution is not something that inexplicably happened.

For some reason, the author has built the book around an attempt to compare the history of evolution with the story of creation according to the book of Genesis. He makes much of this in the introduction, and the book is divided into chapters headed The first day, The second day, etc. However, this purpose seems to have been almost completely forgotten in writing the individual chapters, for only a very few paragraphs have been devoted to it. It seems to have been used as a framework by which to outline the book and then to have been put aside.

There is an index of five pages and a number of fairly good drawings, some of which are taken from illustrations in well-known scientific works.



A NEW EARTH AND A NEW HUMANITY.

By Oliver L. Reiser. *Creative Age Press, New York.* \$2.50. 8 x 5; xiv + 252; 1942.

This treatise might well have been entitled "A New Philosophy for the Average American." The central theme around which this discourse revolves is that our scientific and technological progress has so outstripped our ethical and social progress that we find ourselves as a race heading certainly and rapidly for extinction unless some drastic change is brought to bear on world conditions. A factor contributing strongly to this situation is the confusion and uncertainty characteristic of our modern system of education. This weakness of our educational system has been in a large measure the direct result of disagreement over *what* should be taught in our schools, and *how* it should be taught. Another contributing factor to our failure in ethical and social progress is that we have not applied enough of the scientific method to these realms of human endeavor. In this connection, the author feels that it is well to remember that the essence of the scientific method is freedom in word and action and that the final authority rests not with a man or an accepted point of view, but with the experiment. It is the belief of the author that when the scientific method is more thoroughly applied to the development of governmental systems, world economy, and social behavior, then and *only then* can we hope to bring any sort of order out of the present chaos. Since America alone retains some vestige of freedom,

the author believes that the American people have a great responsibility in shaping the future destiny of world civilization.

The discussion is timely, and although it may appear to some readers to be slightly tinged with war-time propaganda, we believe that the author is entirely sincere in his viewpoint, and that he has given a great deal of honest, unemotional thought to present world conditions.

The work carries a 25-page index.



THE ARCH LECTURES. *Eighteen Discourses on a Great Variety of Subjects Delivered in New York during the Winter of 1940.*

By Claude Bragdon. *Creative Age Press, Inc., New York.* \$2.00. 8 x 4½; vii + 239; 1942.

The author, an architect by profession, and an educator and philosopher by inclination, here presents a series of discussions which he gave before "The Friends of Carman Barnes Club" in New York City. These lectures, like much of Bragdon's other writings, expound in sincere and convincing manner the so-called "new philosophy" of education, which would supplant the rather mechanistic and materialistic present methods and procedures with other methods and procedures designed to educate the young by stimulating and developing the imagination, the spirit, the aesthetic and cultural senses. With much of the material covered by these lectures the average intelligent reader will disagree violently, but he cannot help but find the author's presentation challenging and enlightening. In certain respects, it is to be hoped that parts of this book will prove to be prophetic. Some of the more interesting lectures are concerned with: yoga, the fourth dimension, symbols and sacraments, archetypes, art and the machine age, skyscrapers, harnessing the rainbow, the theatre, footprints of the eternal fugitive, the ritual of play, the androgyne, modern idolatry, and Emerson—the mouthpiece of the American spirit.

There is neither index nor bibliography, but the book is illustrated with a number of very fine photographs. This reviewer recommends the volume to thoughtful and progressive-minded readers, who will doubtless find in it a picture of the type of world we could all have if we were only willing and able to rise from our present grossly materialistic level of living to the higher plane of the idealistic.



BASIC LABORATORY PRACTICE: *An Elementary Manual of Fundamental Technic.*

By Norman G. Sprague. *Chemical Publishing Company, Brooklyn.* \$3.50. 8½ x 5½; ix + 124; 1941. This book is a new type of chemical laboratory manual

designed to accompany any laboratory course book. The author here gives concise and collected form to numerous elementary details and instructions of laboratory behavior and technique which are not usually found in one place, and many of which are probably gathered only by word of mouth. The purpose is twofold: to aid the instructor in a burdensome, though important, task, and to give the student the continual detailed instruction in good laboratory technique which is so vital to success. The manual is in no way a collection of trick methods, "kinks", short-cuts, or improvisations. The student is expected to use a little originality, and the instructor to present better methods, if he knows them. The arrangement of the contents is as follows: rudiments of behavior and technique, preparation of some very simple and essential equipment, some general operations with liquids and solutions, filtration, dish-washing, drying and absorption apparatus, use of the chemical balance, a few volumetric manipulations, and chemicals that entail special difficulties and dangers. The author concludes with a discussion of study, including study habits, literature of chemistry, notebooks, reports, the spoken word, and honesty. The book is appropriately illustrated with photographs and drawings, which add greatly to its value for the student, and concludes with an index. There is little doubt but that this manual will be a real boon to the chemistry instruc-

tor and of invaluable assistance to the student throughout his entire chemistry course.



PHOTOGRAPHY: Its Science and Practice.

By John R. Roebuck and Henry C. Staehle. D. Appleton-Century Company, New York and London. \$5.00. 8½ x 5½; xv + 283; 1942.

The present volume is a survey of the modern science of photography as it is understood and practiced today. Topics such as the nature of the photographic emulsion, exposure and development, color sensitivity, chemistry of the photographic process and positive processes such as printing, enlarging, and the making of lantern slides, etc., are treated in detail. The latest views on the mechanism of image formation are presented in a chapter entitled "Theory of the latent image," and one chapter is devoted to lenses and the optical aspects of photography. Of considerable interest is the account given of the principles involved in the various processes of color photography. Since the object of most photography is to obtain good pictures the authors have very appropriately given us, in a final chapter, many practical suggestions as to composition.

A very useful laboratory manual of practical experiments and a general bibliography conclude the volume.



THE QUARTERLY REVIEW of BIOLOGY



THE NEW PERSPECTIVE IN THE HALOPHYTES

By V. J. CHAPMAN

I. INTRODUCTION

A SUMMARY of the recent literature on the halophytes appeared in the *Botanical Review* for 1941 (Uphof), but it would seem that there is still need for a critical discussion of the more important recent papers, some of which have appeared since the review referred to above. The object of such a discussion would be first, the assessment of those phases in which progress has been most pronounced, and second, an indication of the direction along which future research might profitably proceed.

Stocker (1928) has defined halophytes as "those plants which at any stage of their life are subjected to a concentration of salt [*Salzwirkung*, in the original] which is more than 'normal' glycophytic plants can bear without dying." (Glycophyte is a convenient term for all plants that cannot grow in places where the concentration of sodium chloride in the soil solution is more than 0.5 per cent. It must be understood that this is a purely arbitrary definition.) While it may be easy to distinguish between extreme halophytes and glycophytes it is by no means so easy to determine to which class a plant should belong at the lower concentrations of sodium chloride. Field observations and experimental work indicate that the boundary should be placed at about 0.5 per cent sodium chloride in the soil water. Among plants there appears to be a marked difference in tolerance above and below this concentration.

At this point it is essential to define the terms that it is proposed to employ subsequently.

Halophyte. A general term which includes all plants that are capable of growing in an environment where there is more than 0.5 per cent sodium chloride. Its use will not imply that the species is either common or rare in such habitats nor will the term involve the assumption that a plant cannot grow under any other conditions. The Halophytes will not include plants that grow in places where the soil is characterized by an excess of a salt other than sodium chloride, e.g. inland areas where there is an excess of magnesium salts, etc. The flora of such places should be distinguished from halophytes, as defined above, and the plants should be placed in another category. In the past they have commonly been included in the halophytes.

Euhalophyte. This term will be restricted to those plants whose optimal growth takes place in an environment in which there is more than 0.5 per cent sodium chloride. (It is impossible to define more accurately the term "optimal growth." We cannot say growth to maturity because plants may flower and set seed and yet be weakly or stunted. Whilst field observations may indicate whether growth is approaching optimum or not, experiment must ultimately be the decisive factor.) Euhalophytes will not grow unless there is an abnormal concentration of sodium chloride in the habitat. This class includes species of *Salicornia*, *Rhizophora*, and the 'submerged' halophytes, e.g. *Zostera*, *Cymodocea*, *Posidonia*.

Miohalophyte. This will be applied to those plants which are to be found, either commonly or rarely, in habitats where there is more than 0.5 per cent sodium chloride; their optimal development occurs, either naturally or experimentally, in an

environment where there is less than 0.5 per cent sodium chloride (cf. below).

It must be admitted that in many cases we do not yet know whether a species is an eu- or miohalophyte; for such plants we must therefore use the non-committal term of halophyte. In 1939, Van Eijk suggested that what I call miohalophytes could be divided into two classes.

a) Plants which normally grow under glycophytic conditions but which nevertheless have some resistance to a concentration of more than 0.5 per cent sodium chloride. The evidence is based either upon growth in culture solutions or else upon records of occasional plants growing in a halophytic environment. This group can be termed the *haloglyphytes*, and then the true *miohalophytes* will form the second group.

b) Plants which normally grow on haline soils, but whose optimal development is under glycophytic conditions. This category includes a very large number of plants that grow around sea shores, e.g. *Aster Tripolium*, *A. subulatus*, *Triglochin maritimum*, *Plantago maritima*, *P. oliganthos*.

The evidence which is slowly accumulating suggests that the large majority of halophytes are really miohalophytes and that the euhalophytes form a relatively small class. One of the most important results of recent experimental work has been to show that halophytes grow as well, or often even better, under purely glycophytic conditions. The submerged marine phanerogams, together with one or two genera such as *Salicornia* and *Arthrocnemon*, form the bulk of the euhalophytes. A large number of the miohalophytes occur in haline areas because they are unable to compete successfully with glycophytes in non-haline areas. Anyone who attempts to grow miohalophytes under both haline and glycophytic conditions cannot help but observe that the plants are relatively slow growing as compared with the majority of glycophytes: this is true not only of the herbaceous species but also of the woody ones. Serious competition between species only occurs under glycophytic conditions because when there is more than 0.5 per cent sodium chloride present the glycophytes do not grow. Germination may be excellent and rapid, e.g. *Aster* spp., *Salicornia* spp., and even early seedling growth may be good, e.g. *Rhizophora*, *Avicennia*, but it is not long before the growth rate slows down, and under glycophytic conditions the halophytes are soon surpassed and crowded out by other species. In fact halophytes

can only be grown successfully under such conditions so long as they are kept free from competition. This phenomenon may also be correlated to a very large extent with the fact that most of the halophytes are perennials.

There is, however, a further complication. There are those plants which grow on sand dunes near the sea shore: the roots of such plants will commonly be in fresh water, since Oliver (1924), Hill and Hanley (1914) and Chapman (1937) have all demonstrated the presence of a fresh-water table in maritime dunes. The surface of the sand, however, may contain some salt from spray, and the aerial portions of the plants will also be subjected to spray in stormy weather. Stocker (1928) has suggested that the term *xero-halophyte* should be reserved for the plants of the salt (sodium chloride) desert, and that the term *aero-halophyte* should be employed for plants that are subjected to salt in the form of either spray or powder. Schratz (1934), on the other hand, regarded the dunes as xero-haline in contrast to the *hygro-haline* habitat where there is a salt-water table. Examples of plants growing on the former are *Arenaria peploides*, *Psamma arenaria*, *Eryngium maritimum*, and in the latter any of the salt marsh plants, e.g. *Limonium vulgare*, *Triglochin maritimum*, *Spergularia marginata*, etc. There would seem, however, to be no reason for departing from Stocker's earlier usage of these terms.

The degree of salt which a plant is able to withstand has been used by Iversen (1936) as a basis for a classification of salt marsh plants, and by widening the scope it could well be employed for the halophytes as a whole. In many respects it is more convenient because it is dependent upon a feature which can be measured in the field; van Eijk's two classes (cf. above), on the other hand, are dependent upon a knowledge of the growth conditions of the plant, and it cannot be said that adequate studies have been made of many species. Iversen's schema is based upon the amount of sodium chloride present in the soil water table, but since the roots of many plants do not reach down to this depth a more satisfactory criterion would be the percentage of Cl^- present in the soil water at the absorbing region. This classification will include plants from any habitat; furthermore, allowance can be made for seasonal changes in the environment (annual range) and this is an additional feature in favor of the scheme. On this schema,

which has been modified somewhat from the original, there are five groups:

Miohalophytes

1. *Glyco-mesohalophytes*. Plants that grow in habitats with a range of 0.01–1.0 per cent sodium chloride.
2. *Euryhalophytes*. Plants that grow in habitats with a range of $0.1 < 1.0$ per cent sodium chloride.

Euhalophytes

3. *Mesohalophytes*. Plants that grow in habitats with a range of 0.5–1.0 per cent sodium chloride.
4. *Meso-euhalophytes*. Plants that grow in habitats with a range of $0.5 - < 1.0$ per cent sodium chloride.
5. *Euhalophytes*. Plants that grow in habitats with more than 1.0 per cent sodium chloride. (The term is not used again in this sense.)

Summarizing we can say that the term 'euhalophyte' should be restricted to those plants that can grow or reach their optimal development only so long as there is more than 0.5 per cent sodium chloride present, e.g. the meso-, meso-eu- and euhalophytes of the scheme above. All other plants which commonly grow under haline conditions, but which reach their optimal development in a fresh-water environment are to be regarded as *miohalophytes*. The terms *hygrohalophyte*, *xerohalophyte* and *aerohalophyte* may remain in use purely as a means of distinguishing groups of plants that commonly grow under certain ecological conditions.

II. SUCCULENCE

A characteristic of a large number of halophytes is the abnormal development of parenchymatous tissue which brings about the appearance known as succulence. (Parenchymatous tissue has been called internal water storage tissue, and it develops from the hypodermis or tissues beneath; although this may remain a convenient term it would no longer be correct in every case to regard its function as that of water storage.) The condition of succulence has attracted the attention of morphologists in the past but only recently are we beginning to understand this problem. Various workers (Batalin, 1886; Lesage, 1890; Holtermann, 1907; Chermezon, 1910; Keller, 1925; Schratz, 1934) have all shown that there is a relation between the amount of sodium chloride present in the environ-

ment and the degree of succulence (total water content/superficial surface). Although it is possible that excess of sodium chloride is mainly correlated with the development of succulence in halophytes, it must not be forgotten that the phenomenon can be induced by other means and that in nearly every case a proportion is determined genetically. Succulence, for example, has been produced in *Tradescantia* by nitrogen starvation (Chapman, 1931), while Pearsall and Ewing (1929) have been able to bring it about by employing excess nitrogen. Succulence is also a prominent feature of certain desert plants, and here there is evidence to show that it is related, in those species investigated, to a peculiar form of metabolism, known as acid metabolism. This acid metabolism is not a common feature of halophytes although it is known to occur to some extent.

Experiments carried out by van Eijk (1939) have shown that the degree of succulence in *Salicornia herbacea* agg. is determined largely by the Cl^- ion independently, to some extent, of the other cations to which it is attached. It is true that as long ago as 1928 Stocker had expressed the view that the development of succulence was due to the action of specific ions rather than to changes of osmotic pressure, but no quantitative work appears to have been done until van Eijk's study. This is of such importance that it is perhaps worth while reproducing the data (Table 1).

If the operation of the different cations (upper half of table) is compared, it will be noted that the Cl^- ions have a distinct effect upon succulence in comparison with the NO_3^- and SO_4^{2-} ions. Sodium chloride, however, appears to operate in a special way, because a very high concentration e.g. $\frac{1}{2}$ mols., produces a large effect on the degree of succulence, although there is a considerable degree of variation: this phenomenon is also suggested in mixtures with potassium chloride, calcium chloride and sodium sulphate where there is a high proportion of sodium chloride. Apart from the Na^+ ion it seems that the Ca^+ ion also may have an effect upon succulence, because it produces a considerable increase at $\frac{1}{2}$ mols. concentration, though here again the degree of variation is considerable. We may note too that the degree of succulence is raised by the NO_3^- anion when mixed with Cl^- , especially when the former is in excess, so long as sodium is the cation. The SO_4^{2-} anion, however, has a marked depressant effect either alone or in combination with Cl^- ions. The importance of

these results lies in the emphasis that has to be laid on the combined effect of the individual ions, and it is clear that future work on the halophytes must depend largely upon more detailed studies of the ions and their effects. This is a point that will be referred to later, but some surprise may be expressed that this important phenomenon in the halophytes has been more or less overlooked during the last twelve years. At present it is not clear exactly how the ions, either alone or in combination, achieve their specific effects; it is possible that they have some effect upon the biocolloids in the cell walls, and future work might well be turned in this direction. Another possibility is that the

that there was no great change in succulence as the concentration of Cl^- ions increased. There is some evidence, however, that the leaves of mangroves are more succulent under certain conditions (Walter and Steiner, 1936; Holtermann, 1907).

Before leaving the problem of succulence we may refer again to the possibility that acid metabolism may in certain cases be concerned in promoting succulence in halophytes. At present far too few examples have been investigated for us to make dogmatic statements about the cause of succulence. Plants, in which a high concentration of certain ions is suspected of being the causal factor, when grown under conditions in which the ions are

TABLE 1
*Degree of succulence in Salicornia herbacea grown in different salt solutions**

CONC. IN MOLES./LITRE	NaCl	KCl	CaCl ₂	MgCl ₂	NaNO ₃	Na ₂ SO ₄
0/0	33 ± 1.0	33 ± 1.0	33 ± 1.0	33 ± 1.0	33 ± 1.0	33 ± 1.0
1/12	36 ± 1.5	39 ± 1.2	40 ± 1.0	41 ± 1.4	36 ± 1.8	36 ± 0.9
2/12	39 ± 2.1	29 ± 1.2	47 ± 3.0	42 ± 1.4	37 ± 1.7	—
4/12	45 ± 1.2	42 ± 1.0	—	45 ± 2.0	34 ± 1.2	36 ± 0.3
6/12	43 ± 1.1	43 ± 1.1	—	—	—	—
8/12	51 ± 4.0	42 ± 1.0	—	—	—	—

PROPORTION OF MIXTURES**	NaCl/KCl	NaCl/CaCl ₂	NaCl/MgCl ₂	NaCl/NaNO ₃	NaCl/Na ₂ SO ₄	
4/12	3:1	52 ± 5.3	47 ± 1.3	44 ± 2.3	43 ± 2.0	46 ± 2.2
	1:1	47 ± 4.2	46 ± 1.7	—	—	—
	1:3	47 ± 2.8	42 ± 1.9	46 ± 1.5	48 ± 4.3	41 ± 1.7
8/12	3:1	46 ± 2.1	—	—	—	—
	1:1	44 ± 2.6	—	—	—	—

* There was also a basic culture solution from which these salts were otherwise absent.

** Basic value 33 ± 1.0 in pure culture solution.

development of mucilages in the plant cells may be correlated with the presence of the ionized salts. Van Eijk (1939) very pertinently points out that it must be the accumulation of the individual ions in the growing parts of the plant that has such a profound effect upon its structure. This, however, is not the whole story. Walter and Steiner (1936) have shown that there is a low percentage of sodium chloride in the seedling tissues of *Avicennia marina* and *Rhizophora mucronata* when on the tree, but that it increases rapidly very soon after the seedling has fallen to the ground. The present author working with seedlings of *Avicennia nitida*, *Laguncularia racemosa* and *Rhizophora mangle* found the same phenomenon, but a morphological examination of an age series of *Avicennia* seedlings indicated

absent do not necessarily lose their succulent character. It would seem that there is a basic degree of succulence, which is determined genetically, and that an increase in the degree of succulence can be super-imposed upon the genetical quantity by other external or internal factors (e.g. ions or acid metabolism). The problem is rendered even more complex by the fact that such features of the environment as temperature may influence to an appreciable extent the interaction of the ions (Mevius, 1927). Future work should aim at 1) establishing the degree of succulence which is genetically controlled; 2) ascertaining the primary causes of any superimposed succulence, together with the effect of the environment; and 3) determining the effect of any environmental factors.

III. DIFFERENTIAL ABSORPTION OF IONS

For some years it has been known that certain plants, and indeed probably all plants, do not absorb any one electrolyte in its molecular proportions but that either the anion or the cation will be absorbed to a greater extent. Such a process, of course, involves maintenance of the charges within the cell by the loss or addition of an equivalent quantity of other ions of the opposite sign to the ion concerned. It is evident that the work on this aspect, together with the results of van Eijk on the effect of different ions, reopens and enlarges the vista surrounding the halophytes. Even more important, however, will be the concentrations of

ride because of the great excess of this salt in sea water (Fig. 1). One feasible explanation that offers itself is that the sodium and chloride ions are held to different extents by the soil colloids and that the sodium ions are more tenaciously bound than the chloride (we have to assume that no greater quantity can be extracted by the plant than by the soil chemist). This may mean that there is a more ready supply of chloride ions for the plant than there is of sodium, so that theoretically there is the possibility that the plant may absorb rather more of the former than of the latter. This would result in a differential proportion of these ions in the plant tissues; as there seems to be a pre-

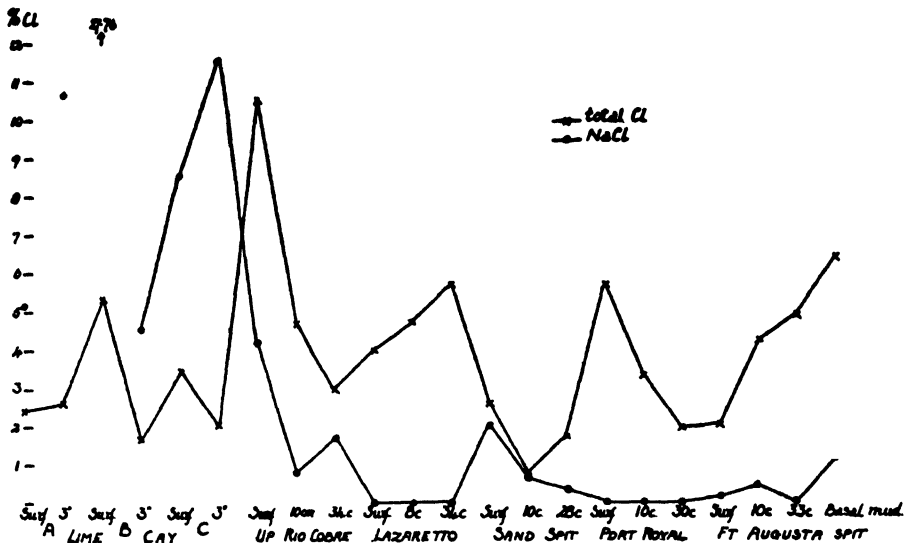


FIG. 1. TOTAL CHLORIDE AND CHLORIDE EQUIVALENT OF THE EXCHANGEABLE SODIUM IN SOME SOILS FROM JAMAICAN MANGROVE SWAMPS

the various ions within the plant tissues, because upon these will depend the nature and quantity of any more that may be absorbed. If we take our analysis yet further we ought to consider whether the ions are present in the sap or the cytoplasm of the individual cells. There is thus a whole chain of inter-relationships about which relatively little is known. The present author has shown (1939, 1940 and in prep.) that among the salt marshes of Norfolk and New England and in the mangrove swamps of Jamaica the amount of exchangeable sodium in the soil (estimated by a standard method of soil analysis) will not account by any means for the total quantity of chloride available, though in such soils we must suppose that the bulk of the chloride will be present originally as sodium chlo-

ride because of the great excess of this salt in sea water (Fig. 1). One feasible explanation that offers itself is that the sodium and chloride ions are held to different extents by the soil colloids and that the sodium ions are more tenaciously bound than the chloride (we have to assume that no greater quantity can be extracted by the plant than by the soil chemist). This may mean that there is a more ready supply of chloride ions for the plant than there is of sodium, so that theoretically there is the possibility that the plant may absorb rather more of the former than of the latter. This would result in a differential proportion of these ions in the plant tissues; as there seems to be a pre-

disposition for chloride ions to be more readily available in the soil water than sodium so one might expect that the effect produced by the former would be more evident than that produced by the latter. The problem is not quite so simple. There is no evidence that the plants absorb the two ions in the same proportions that they are available in the soil: the current evidence all points to the contrary. Analyses of soils and portions of plants (whole tissues) of *Avicennia nitida* showed that though in both cases there was an excess of total Cl^- ions over the amount that theoretically should be present as sodium chloride (based on analyses of exchangeable sodium), nevertheless the excess was appreciably smaller in the case of the plant organs. This fact resulted in a complete lack of correlat

between the ion contents of the soil and corresponding plant tissues over a range of habitats, but the explanation of this phenomenon may well be that suggested above (Fig. 2). The reverse was found in the case of *Salicornia herbacea* because there was a greater excess in the plant tissues as opposed to the soil in which the plants grew (Fig. 3). We may note that *Salicornia* with the greater excess of Cl^-

method used in analysis of total Cl^- : uranyl zinc acetate method in obtaining amount of exchangeable sodium) of internodes, rhizomes and leaves of two plants each of *Phragmites* from a salt marsh, an old reclaimed salt marsh, from a fresh-water habitat and from an area where the reed was actively colonizing a salt marsh. The first point to be noticed is the variation in distribution in the

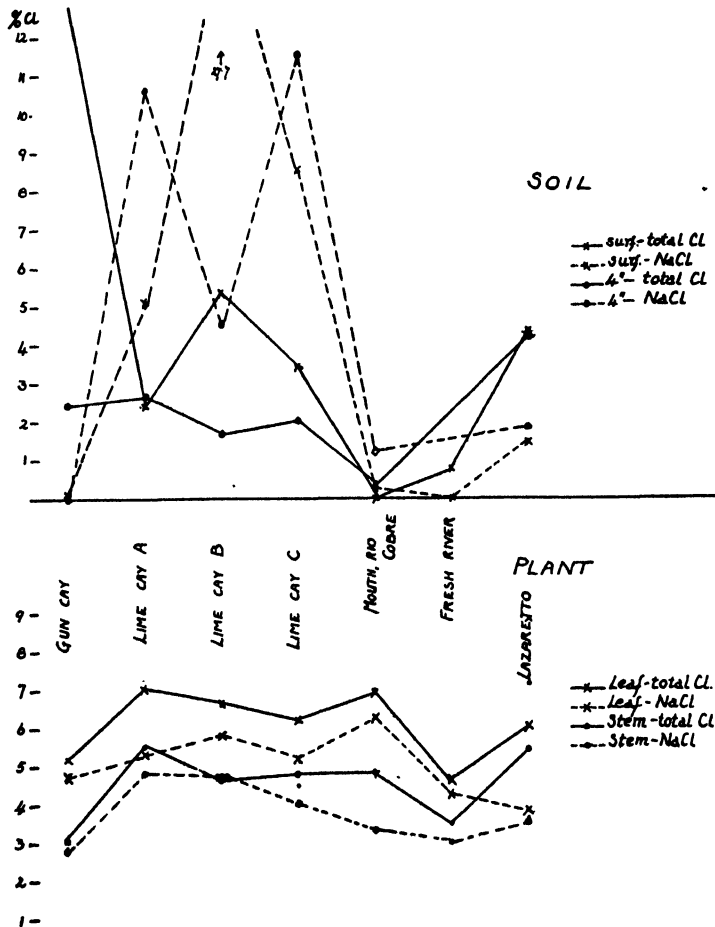


FIG. 2. RELATION OF TOTAL CHLORIDE AND CHLORIDE EQUIVALENT OF THE EXCHANGEABLE SODIUM IN PLANT TISSUES OF *AVICENNIA NITIDA* COMPARED WITH THE PROPORTIONS IN THE SOILS SURROUNDING THE PLANTS

ions is a pronounced succulent, whereas *Avicennia* with a smaller excess is not; we must remember, however, that nothing is known about the other ions that may be present in the plant tissues. An investigation into the differential distribution of the sodium and chloride ions in plants of *Phragmites communis* from different habitats showed that the type of environment may influence the internal distribution of these ions. In Fig. 4 are depicted analyses (potassium permanganate

various tissues, e.g. in all four habitats there is an excess of total Cl^- in the rhizome: in some habitats there is an excess of total Cl^- in the leaves and in others an excess of exchangeable Na^+ , i.e. there is more than sufficient Na^+ ions to account for the total Cl^- ions present. In the leaves of the marsh *Phragmites* there is an increasing excess of exchangeable Na^+ ions up to the apex, whereas in the fresh-water plant there is no great variation but there is a slight excess of total Cl^- in all the leaves.

The leaves of the colonizing *Phragmites* show a pronounced increase in the excess of total Cl^- towards the apex, while in the plants from reclaimed marsh there is an excess of exchangeable Na^+ at the base and of total Cl^- at the apex. The distribution of ions in the nodes, though not so spectacular, also shows considerable variation. In the marsh plants there is a slight excess, which does not vary greatly, of Na^+ in the upper nodes, while in the fresh-water plant there is a slight excess of total Cl^- throughout. The colonizing plant is again the most interesting with an excess of exchangeable Na^+ ions at the base leading to a reversal and an excess of total Cl^- at the apex.

commence by having a large excess of total Cl^- , but by the end of the year the position is reversed and there is an excess of exchangeable Na^+ ions; similarly the considerable excess of total Cl^- found in the rhizome of the seedling is reduced to a negligible quantity in the adult by November. Not only, therefore, does the environment have to be considered but also the season of the year and the plant tissue. In this particular case no data are available to show whether the ontogenetic drift is correlated with changes in the degree of succulence.

One is forced to the conclusion that much of our work on the halophytes and their behavior will have to be repeated in the light of these preliminary

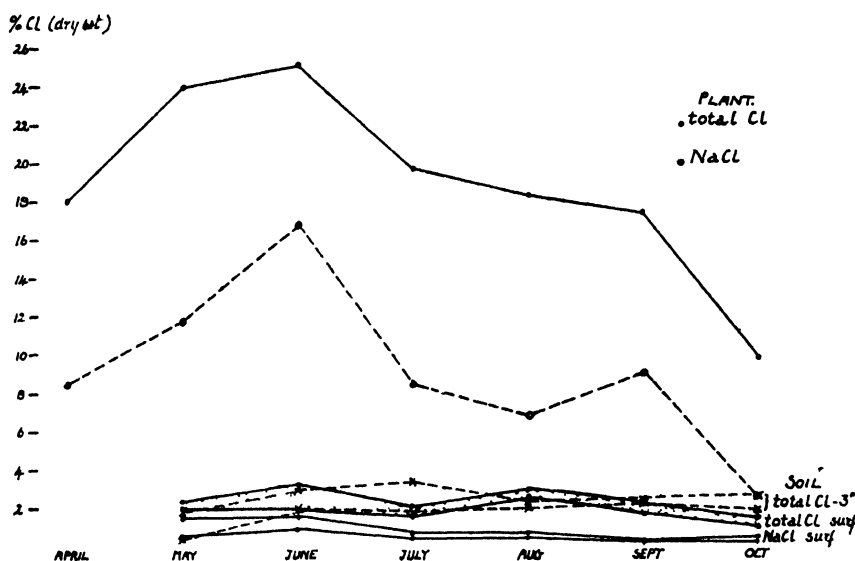


FIG. 3. RELATION OF TOTAL CHLORIDE AND CHLORIDE EQUIVALENT OF THE EXCHANGEABLE SODIUM IN PLANTS OF *SALICORNIA HERBACEA* COMPARED WITH THE PROPORTIONS IN THE SURROUNDING SOIL

This is not the place to consider how these results are related to the different environments, but they are important because they demonstrate the profound effect that the type of habitat may have upon the distribution of certain ions within plant tissues. Again this is an aspect about which we know remarkably little.

Before leaving this subject we may refer to seasonal changes in the distribution of the Na^+ and Cl^- ions in different tissues. In Fig. 5 the annual drift of these two ions during the first year's growth of comparable and even-aged plants of *Aster Tri-polium* shows that the leaves have an excess of total Cl^- which gradually decreases towards the end of the year. The well-marked seasonal optimum in August is also worth noting. The roots

results. Apart from the little we know about the behavior of the Na^+ and Cl^- ions there is a considerable number of other ions which have scarcely been investigated in relation to their effect on morphology. So far we only know something about the effect of one or two individual ions on a few species, while we know much less about the distribution of these ions in the halophytic soils and hardly anything about their absorption by the plants. On the other hand it does seem that an attack along these lines should yield extremely valuable information and enable us to obtain a better grasp of the halophyte problem as a whole.

We may also briefly consider here the phenomenon of salt accumulation against a gradient and its effect on root respiration. In those plants where

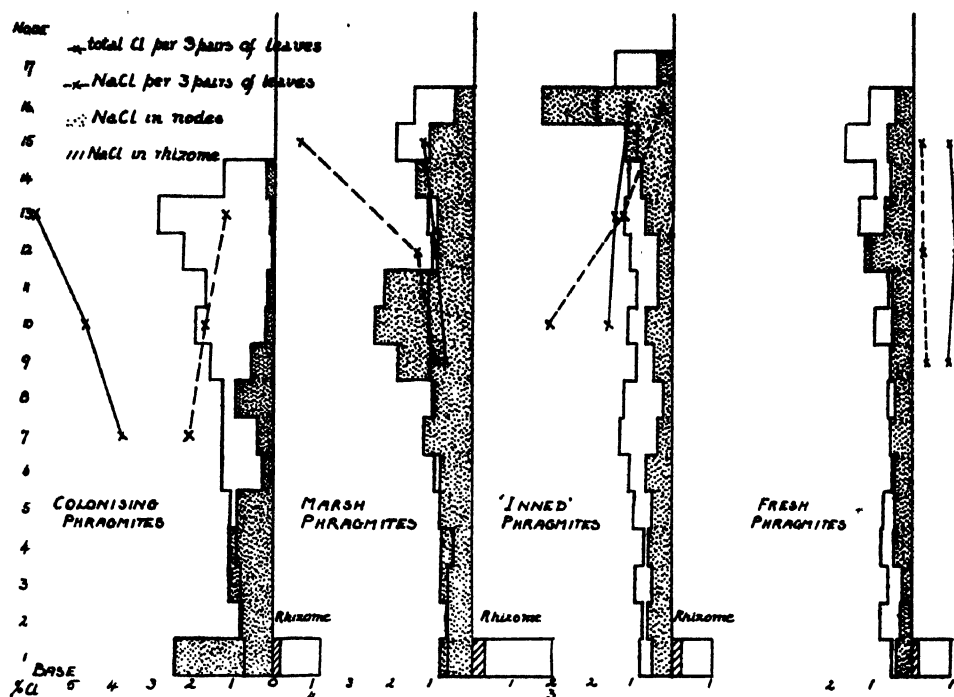


FIG. 4. DISTRIBUTION OF TOTAL CHLORIDE AND CHLORIDE EQUIVALENT OF THE EXCHANGEABLE SODIUM IN PLANTS OF PHRAGMITES COMMUNIS FROM DIFFERENT HABITATS

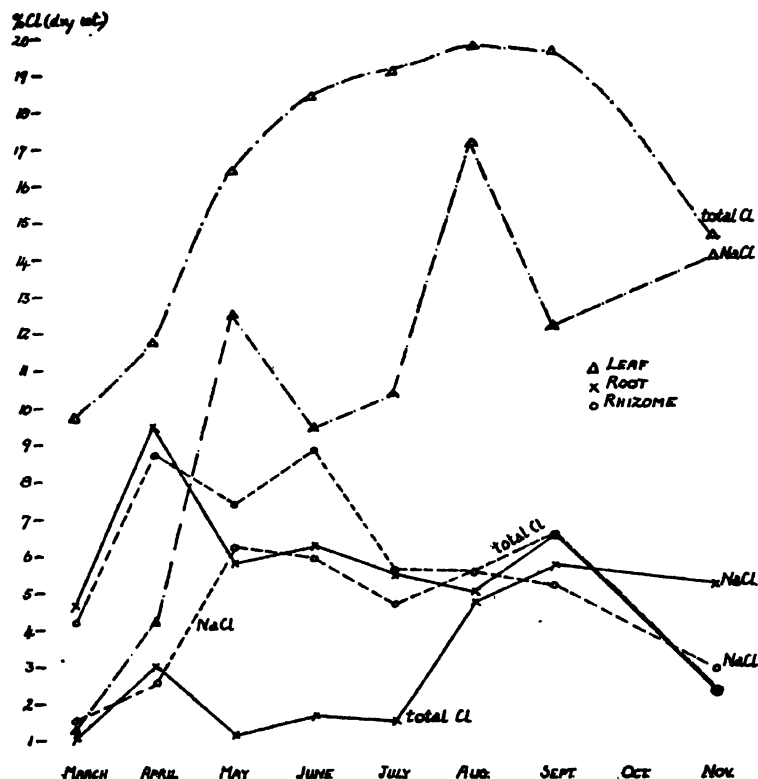


FIG. 5. ANNUAL DRIFT OF TOTAL CHLORIDE AND CHLORIDE EQUIVALENT OF THE EXCHANGEABLE SODIUM IN FIRST YEAR PLANTS OF *ASTER TRIPOLIUM*

there is an accumulation of one or more ions against a gradient work must be done if the process is to take place. We know that such an accumulation of sodium and chlorine does occur in halophytes so that we are forced to conclude that the necessary work must be done. At this point we have to consider two rival theories; those of Steward (1935) and L  ndeg  rth (1939). The former postulates that the extra energy for this work is provided for by an increase in the general level of respiration, while the latter argues that there is a special increase, which he terms the 'anion respiration.' At present the position is more or less fluid and further study of the halophytes should materially contribute towards a definite decision. It is not impossible, of course, that both theories may be correct, and that what is really required is a determination of the proportionate part that each plays. Van Eijk (1939) has come to the conclusion that the energy for salt accumulation in the roots of *Aster Tripolium* is largely provided for by an anion increase in respiration, though there may be a small cation component. This, however, represents results from a single species and others require investigation before this problem approaches solution.

IV. REGULATORY MECHANISMS OF OSMOTIC PRESSURE

This is a problem of which only the fringe has been touched, and although both Stocker (1928) and Steiner (1934) have given some attention to it there are many features that still await investigation. Among the halophytes, where osmotic pressure must depend to a large extent upon the excessive amount of sodium and chlorine present, three distinct groups have been recognized.

1. *Succulents*. In this group it is supposed that an increase in the sodium chloride uptake is compensated for by a corresponding dilution of the internal solution. There must, however, be a limit to the amount of water that the tissues can absorb and store, and one would suspect that during the growing season there will in fact be a steady small increase in the osmotic pressure. Unfortunately we do not possess the relevant data. According to Stocker plants of this type will only take so much sodium chloride out of the soil as they can use or tolerate. The regulatory mechanism, however, is not unlimited and after a time the organ ceases to function: in the case of *Salicornia* the water storage tissue dries up leaving only the woody stele. This implies some sort of regulation of absorption, but

there is no quantitative data in support of this hypothesis other than the fact that increases of sodium chloride in the tissues do not proceed at a rate comparable to corresponding increases in the soil. Another possibility is that there may be a great increase in the sodium chloride content during the seedling stage with relatively little later on. This seems especially true of mangroves and reference will be made to it later. As examples of the succulent category we may quote *Salicornia* spp., *Aster Tripolium*, *Arthrocnemum* spp., *Plantago maritima*, *Spergularia marginata*.

2. *Salt excreting forms*. In this group an increase in sodium chloride accumulation is counteracted by a corresponding excretion of the salt by means of special excretory glands, and, according to Stocker (1928), there is no control of uptake in such plants. The existence of these glands has been known for many years, but there is little or no experimental evidence to prove that the amount of sodium chloride excreted is in fact sufficient to compensate for any increase due to absorption. Plants with such salt excreting glands are *Spartina* spp., *Distichlis spicata*, *Glaux maritima*.

3. *Plants which do not appear to have any special regulatory mechanism*. During the vegetative period the osmotic pressure in the leaves gradually rises and reaches its maximum at the end of the season when the leaf dies. While this may be a true picture of what happens in the leaf there still remains unsolved the nature of the changes that are taking place in the perennial rhizome. It is hardly likely that the osmotic pressure here can go on rising without a limit being reached, and one therefore suspects the existence of a regulatory mechanism.

V. THE SOIL ENVIRONMENT

In an earlier paper on this same problem the present author (1936) referred to some results obtained by Steiner (1934), in which it was claimed that the osmotic pressure of the soil water in certain New England marshes varied in such a manner that it could be correlated with the ecological distribution of the vegetation. The measurements, however, were obtained cryoscopically and hence must refer to all the solutes present. Recent work has shown that electrolytes are not available in the soil in their molecular proportions, presumably due to differential colloidal absorption, so that Steiner's results, though interesting, need amplification. Later, Penfound and Hathaway (1938), in a study

of the marshlands of S.E. Louisiana, came to the conclusion that the zones to be observed there were probably controlled by the sodium chloride content, but here again no distinction was made between the action of Na^+ and Cl^- ions.

Walter and Steiner (1936) working in the mangrove swamps of E. Africa have shown that there is a series of isohalines as one passes from the sea edge of a swamp to the bare salina behind. How far these gradations really control the zonation of the adult plants is another problem. The present author has investigated the same phenomenon in

Apart from the mangroves the present author has given some attention to the environment of the salt marshes in Norfolk, England, and at Lynn, near Boston, Mass. In both areas the total chloride content in the different soil layers of the various communities fell to a minimum in the spring when seed germination may be expected to commence. A similar fall has been recorded from a saline habitat in Thuringia, where the percentage of sodium chloride fell from 5.2 per cent in the autumn to 2.8 per cent in the spring. A very recent study (Purer, 1942) of salt marshes near

TABLE 2
Percentage germination of four species after freezing

	SALICORNIA MUCRONATA		SPERGULARIA MARGINATA		SUAEDA MARITIMA		PLANTAGO OLIGANTHOS	
Tap water	30	48	80	90	12	24	5	5
1 per cent NaCl . . .	28	50	100	95	6	10	0	0
2 per cent NaCl . . .	14	14	52	25	2	0	0	0
3 per cent NaCl . . .	2	8	32	0	0	0	0	0
Freezing temp.	-10°C.	-20°C.	-10°C.	-20°C.	-10°C.	-20°C.	-10°C.	-20°C.

TABLE 3
Percentage germination after 28 days

	PERAGHITES COMMUNIS	ASTER TRI- FOLIUS	SPERGULARIA MARGINATA	SALICORNIA HERBACEA	SUAEDA MARITIMA	JUNCUS MARITIMUS	ARTEMISIA MARITIMA
Tap water	4	45	66	93	4	50	86
1 per cent NaCl . . .	32	25	4	45	0	18	8
2 per cent NaCl . . .	16	10	0	36	4	5	0
Sea water (3.3 per cent NaCl)	0	0	0	38	0	0	0
5 per cent NaCl . . .	0	0	0	36	0	0	0
10 per cent NaCl . .	0	0	0	12	0	0	0

the mangrove swamps of Jamaica, and while there is some evidence of a series of isohalines as one travels up an estuary, nevertheless it seems that the adult plant zonation is determined very largely by what takes place during seedling establishment; here there is a whole complex of factors in which salinity probably does not play any major rôle. In the salt marsh, however, the problem is perhaps different: the vegetation is low-growing and often shallow-rooted so that the roots are more subject to changes that can take place in the surface layers of the soil. In the mangrove swamps the shade cast by the trees must reduce the fluctuations in soil salinity to a considerable extent.

San Diego, California, revealed a similar spring minimum. This fact is of extreme importance because experiment shows that the seeds of many species will not germinate under other than low concentrations of salt, and it is the salinity of the marshes at this time of the year which must play a large part in determining the composition of the adult community and the rate of colonization. Stocker (1928) has pointed out that in many apparently haline areas it is only the surface layers that are so salt and that low values are recorded in the layers beneath. In such places plants are only kept out because seeds cannot germinate when lying on the surface soil where the salt content is high. The percentage germination of four species from some American marshes after freezing is shown in Table 2.

Similar germination studies have been carried out by the present author using seeds of British salt marsh plants (Table 3). These were not subjected to freezing because English marshes do not become frozen for a month or more as they do in New England.

From these tables it can be seen that the only species with any tolerance (in respect of germination) of excess sodium chloride is *Salicornia herbacea*, though *S. mucronata* and *Spergularia marginata* from America exhibit only a slightly lesser

degree of tolerance after being frozen. The pre-history of the parent plants, e.g. whether they grew in haline, brackish or fresh-water habitats, is of some importance, not only in determining the percentage germination but also the subsequent seedling growth rate (Fig. 6). In the submerged halophytes adventitious root formation is dependent upon variations in salinity in the surrounding medium, e.g. in *Zostera marina* it will only take place over a narrow range, 1.5–3.0 per cent, while in *Ruppia rostellata* it takes place over a wide range, 0–8 per cent, so that here also different species exhibit different degrees of tolerance. The control exerted by sodium chloride over germination is not the whole problem: not even the euhalophytes will grow in pure sodium chloride solutions, so that balanced media are necessary even for them.

Returning once more to the concentration of sodium chloride in the soil we can note that there may be very definite changes in the vertical gradient at one or more times during the year. These were very pronounced in a study of an American marsh (Fig. 7), and such changes may be of considerable significance in relation to the physiology of the roots. On the whole, however, the tolerance of many halophytes towards excess sodium chloride is much wider than may be expected (Penhallow, 1908; Penfound and Hathaway, 1938). In places where the vegetation is low-growing, rainfall during the summer months may have a profound effect upon the salinity of the surface layers of the soil, and this in turn may be of importance for the roots of small annuals, e.g. *Salicornia* spp. and also those of the grasses, e.g. *Puccinellia maritima*, *Distichlis spicata*, *Spartina patens*. A complex of factors is responsible for the salinity of the soil water at any given season, and hence it is very difficult to determine to what extent salinity itself plays a major part in controlling the zonation. In both Norfolk and New England there is remarkably little evidence of any great variation in the chloride concentration of the soil water as one proceeds from the lower to the higher marshes, because such gradients as one might expect are frequently masked by other factors, e.g. height of vegetation and control of evaporation. Fig. 8, showing variation in salinity during June–August from different communities on such marshes, is instructive, but all the evidence slowly but surely leads to the conclusion that the answer is not to be sought so much in a study of the environment of the adult plants but in a study of the seedling

stages and the process of their establishment. The potent factor may be the concentration of sodium or chlorine in the soil water at this stage, but much of the work will have to be repeated because we must know which ion is concerned. It is evident that detailed studies and analyses of plants during the young stages are the primary requirements.

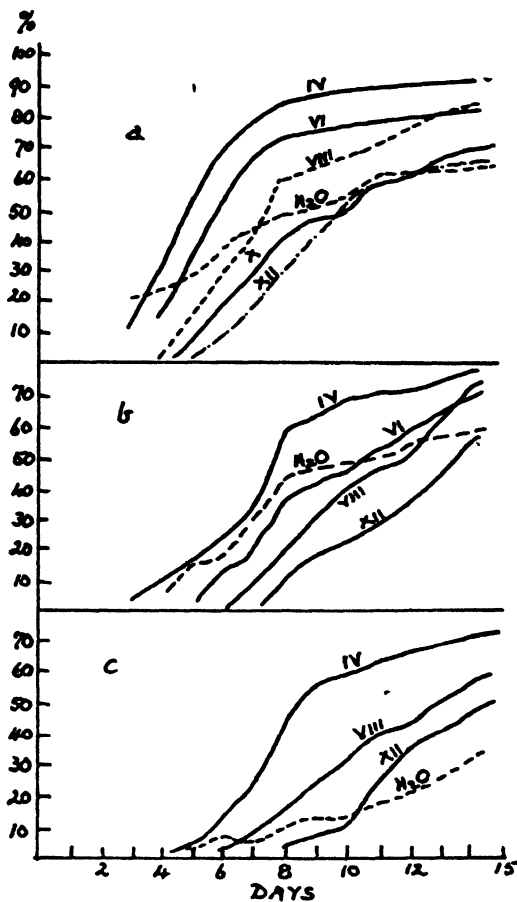


FIG. 6. EFFECT OF DIFFERENT CONCENTRATIONS OF SALT UPON GERMINATION OF SEEDS OF *ASTER TRIPOLIUM*

(a) Seeds from plant in fresh water habitat. (b) Large seeds from plant in saline habitat. (c) Small seeds from plants in saline habitat. The figures on the curves indicate the osmotic pressure of the solution in atmospheres. (After Schratz.)

Apart from sodium chloride, however, there are other soil factors that merit consideration. The movements of the water table may be of profound importance in determining the distribution of certain species. Evidence has accumulated to show that drainage conditions determine whether seedlings of *Obione portulacoides* can grow in a particu-

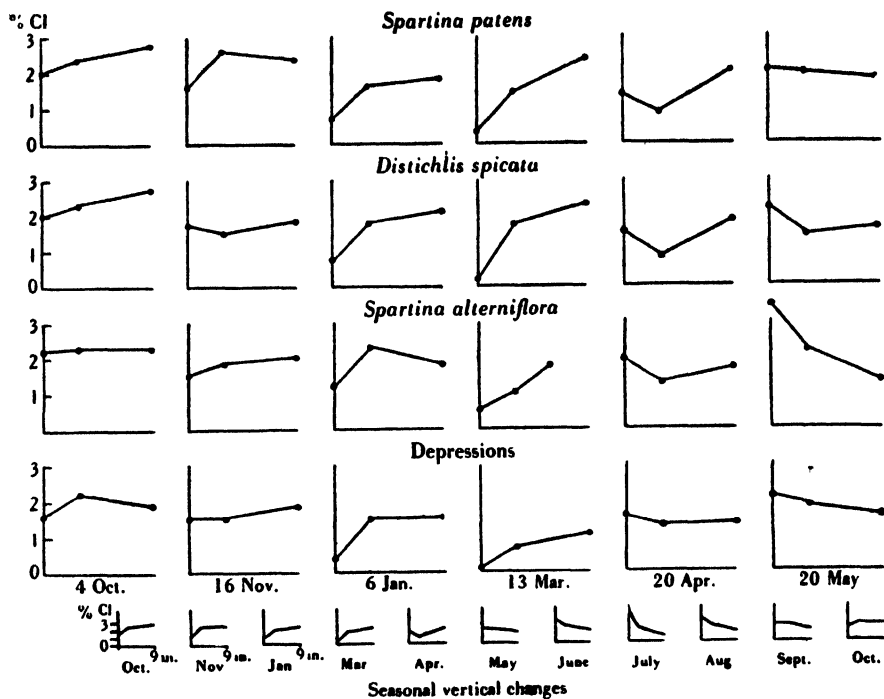


FIG. 7. VERTICAL CHANGES IN TOTAL CHLORIDE IN SOME AMERICAN SALT MARSH COMMUNITIES (After Chapman.)

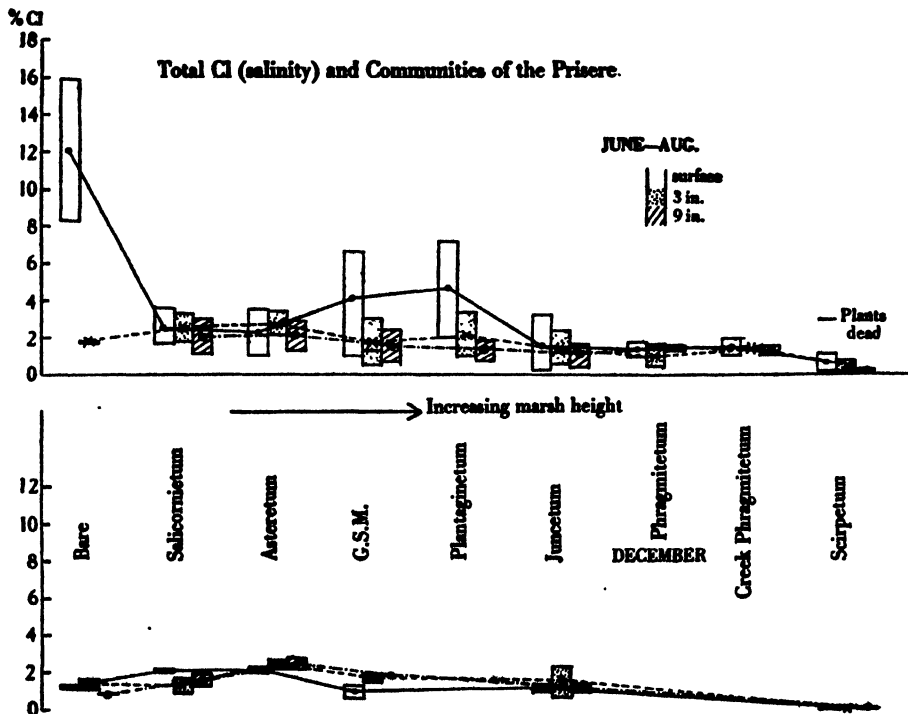


FIG. 8. TOTAL CHLORIDE IN RELATION TO THE SERAL COMMUNITIES ON NORFOLK SALT MARSHES (After Chapman.)

lar area or not. Seedlings which are water-logged experimentally commonly die after a short period even when the operation is carried out *in situ*. The adult plant may sometimes succumb to this treatment, though once plants of this species have passed the seedling stages they become much more resistant. This again brings us back to the great importance of the seedling stage, a phase which perhaps does not at present receive the attention from ecologists which it deserves. The response of the seedling to drainage is the principal reason that *Obione portulacoides* is commonly to be found fringing the banks of creeks on salt marshes, where it has been shown (Chapman, 1938) that the drainage conditions are good: on Holme marsh in Norfolk certain creeks have become dammed and converted into pans by a shingle fan thrown over the marsh by the waves. In these pans, where water now stands for much of the year, many of the adult *Obione* plants have died, and the effect is striking when compared with the unaffected creeks nearby. Another species which also appears to be influenced in its distribution by drainage is *Suaeda fruticosa*, whilst the occurrence of both *Aster Tripolium* and *A. subulatus* is primarily determined by the concentration of sodium chloride in the surface soil at the seedling stage. We need to know far more about the biological responses of the individual species. Future work on the eu- and miohalophytes should be directed to this end rather than to the continued study of communities as such.

We must also re-orientate our outlook upon the subterranean environment of plants growing in salt marshes and mangrove swamps. In the past it has commonly been thought that when the tide floods a marsh all the roots will be waterlogged. Work, both in Norfolk and America, has disproved this, and has shown that over the bulk of the marshes when there is a flooding tide an aerated layer persists just beneath the surface of the soil. This layer varies in depth depending upon a number of different factors, e. g. type of soil (sand or clay), heights of previous tides, distance from creek, etc., but it is important to note that a very large proportion of the total quantity of absorbing roots belonging to the different species will be present in the aerated layer. The occluded gas can be extracted and analyzed, and although much of it may be hydrogen sulphide nevertheless there are measurable proportions of both carbon dioxide and oxygen as the following table (Table 4) will show.

The most striking features are the relatively low values of oxygen, some of which are so low that respiration of the roots may be seriously affected, and the relatively high proportion of carbon dioxide. If the soil atmosphere is in communication with the external atmosphere, as field observations suggest it must be, then diffusion and interchange of the gases cannot take place readily. Although great variations in the concentrations of carbon dioxide and oxygen may be recorded, it must be remembered that in many of the halophytic habitats the soil is so moist that the roots will be surrounded by a definite film of water and first there must be the solution of the gases by this film before

TABLE 4
Analysis of gas extracted from the aerated layer of soil

COMMUNITY	PER CENT CO ₂	PER CENT O ₂	PER CENT RESIDUAL GAS
Asteretum.....	2.99	1.61	95.4
Asteretum.....	2.55	0.82	96.63
Asteretum.....	3.26	0.71	96.03
Asteretum.....	4.22	1.42	94.36
Glycerio-Obionetum...	1.46	10.50	88.04
Glycerio-Obionetum...	0.93	17.50	81.57
Salicornietum on shingle....	0.88	18.30	80.82
Spartinetum alterniflorae..	1.79	3.42	94.79
Spartinetum alterniflorae..	3.23	8.28	88.49
Spartinetum patensis.....	0.58	17.30	82.12
Distichlidetum..	1.17	17.30	81.53

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diffusion into the roots commences. These figures lead one to suggest that an investigation into the respiratory behavior of the roots of salt marsh plants under conditions such as those above should yield valuable results. In the mangrove swamps of the West Indies one can also detect an underground atmosphere, primarily confined to crab burrows and the holes left by rotting roots. In *Avicennia* and *Rhizophora* only the ultimate absorbing roots are exposed to this atmosphere because the rest of the underground system is protected by a thick corky coat, but this may not be true of the roots in other species. The roots, whether protected or not, must exist in a soil atmosphere in which again the oxygen is frequently

very low and the carbon dioxide very high. Here also, as well as in the salt marshes, there is scope for further investigation. No data appear to be available about the soil atmosphere in xero-haline habitats.

Before passing on it may be as well to refer to the mechanical composition of the soil in relation to the vegetation. The present author (1941) has pointed out that the salt marshes of Great Britain can be divided into four groups, and it has been suggested from superficial observation that the differences in vegetation are largely determined by the proportions of sand, clay and silt. The same kind of phenomenon can probably also be observed in the U. S. A., though perhaps to a lesser extent. In any case a study of the vegetation and soils of the Bay of Fundy, New England and coastal plain marshes might prove unexpectedly productive. This is a problem, however, of which only the fringe has been touched, largely perhaps because of the magnitude of its size and the vast areas that would require to be covered. A major survey of marshes on this scale ought to be made, and from present indications it is clear that significant results would be forthcoming.

VI. TRANSPIRATION

Much work has been carried out on the transpiration of halophytes but the results are conflicting because some workers report that they transpire at a faster rate than mesophytes and others that they transpire at a slower. There appears, however, to be no real distinction in transpiration rate between hygrohaline and xerohaline plants. There are at least two papers which indicate lines along which research might profitably extend in the future. In the one, Schratz (1935), using a very sensitive torsion balance and weighing 30 secs. after cutting and again 60 secs. later, found that miohalophytes transpire less than mesophytes, but he goes on to point out that the result obtained depends on the unit of measurement used, e.g. whether it is based on fresh weight or leaf area. In the Genus *Plantago*, the three species *P. maritima*, *P. coronopus* and *P. major* form a series occupying habitats ranging from the halophytic to the purely glycophytic. Measured on the basis of fresh weight *P. major*, the glycophyte, showed the highest transpiration rate and *P. maritima* the lowest, while using leaf area the exact reverse was obtained. In order to overcome this anomaly Schratz suggested that a new unit of measurement

should be employed, which he called the "*wasserumsatz*," that is, the time taken to transpire once the total weight of water contained by the plant. When a glycophyte and a succulent plant are exposed to desiccation for any length of time the transpiration of the former will drop rapidly, whereas that of the latter will tend to be maintained. The occurrence of plants in specific environments is more likely to be correlated to their *wasserumsatz* than to their transpiration rate as measured at a given moment. For the purpose in hand, therefore, the *wasserumsatz* would seem to be the best unit so far devised. The present writer is not aware of any application of this new basis, and one of the desiderata of the future should be its utilization in comparing the behavior of eu- and miohalophytes in relation to glycophytes.

The other paper to which reference must be made is that by van Eijk (1939) in which he shows that for *Salicornia herbacea* agg.: 1) by increasing the concentration of sodium chloride or calcium chloride the transpiration rate is lowered; 2) in the presence of sodium sulphate a high transpiration rate is maintained. Some of the graphs illustrating these points are seen in Fig. 9, and one may conclude from them that the more Na^+ ions are present the greater the lowering of the transpiration rate. This effect might of course be due to the increasing concentration of the Cl^- ions, but it is worth noting that when potassium and sodium chlorides are mixed in the proportion 3:1 the transpiration rate is increased relative to a pure solution of sodium chloride of equivalent concentration. The SO_4^{--} anion seems to have the opposite effect and when present balances the depressant effect of the Na^+ ions. Although Stocker (1928) had suspected that the transpiration of halophytes was controlled to some extent by the action of specific ions, these are the first quantitative data to be secured. These results are very important because they show that the transpiration of all plants from haline habitats will have to be re-studied from this point of view. Not only may the individual ions exert a direct effect but even more important will be the effect of the interaction of all the ions present.

Rather less evidence is available about both assimilation and respiration. Sodium chloride has a marked depressant effect on both processes in glycophytes, and also causes considerable depression in *Honckenya peploides* (aero-halophyte), but much less in *Salicornia* (Neuwohner, 1938). In

the case of assimilation it has been suggested that it is associated with disorganization of the chloroplasts and cell membranes (Montfort, 1926, 1927), but further study is required in order to analyze the effects of the individual ions.

VII. SEEDLING STAGES

Montfort and Brandrup (1927), Schratz (1934) and van Eijk (1939) have all studied the effect of sodium chloride upon the germination and growth of seedlings of certain salt marsh plants. In the

however, the previous history of the parent plant (e.g. type of locality in which it grew) may have a considerable influence upon subsequent growth of the seedling. We may note also that with increasing concentration of sodium chloride there is an increase in the death rate among the seedlings, but this is to be expected. Apart from the effect on germination van Eijk was able to show that the Cl^- ions, together probably with certain other cations and anions, exerted a controlling influence upon the form and develop-

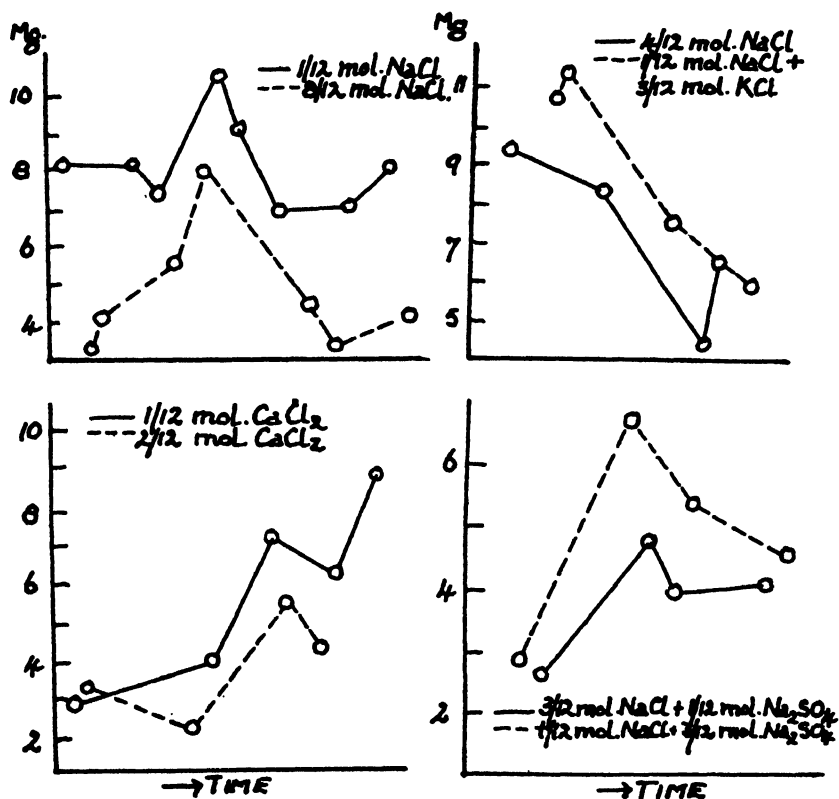


FIG. 9. THE EFFECT OF DIFFERENT CONCENTRATIONS OF SOLUTIONS OF VARIOUS SALTS UPON THE TRANSPIRATION RATE OF *SALICORNIA HERBACEA* (After Van Eijk.)

case of *Aster Tripolium* it was found that optimum conditions for seedling development lay between fresh water and 0.39 per cent sodium chloride, and this has also been confirmed by the present writer. *Aster subulatus* from the American east coast marshes is even less tolerant of sodium chloride.

Montfort and Brandrup and van Eijk have also studied seedling development in *Salicornia herbacea*, and they find that the optimum conditions for growth lie between a concentration of 2.0 and 2.5 per cent sodium chloride. In some species,

however, the previous history of the parent plant (e.g. type of locality in which it grew) may have a considerable influence upon subsequent growth of the seedling. This influence could not be due to the increasing osmotic pressure of the medium because in a series of solutions of sodium sulphate the osmotic pressure rose from 5–16 ats. without bringing about any effect. Above a concentration of 2 per cent sodium chloride the Cl^- ion appears to be a limiting factor. Generally speaking Na^+ seems to be the most favorable cation for growth, though it may also be promoted at low concentrations by increases in either Mg^{++} or NO_3^- ions. In nature, however, many euhalophytes, and prob-

ably all miohalophytes, are to be found growing in areas where the percentage of sodium chloride in the soil water is more than optimal, although one must also consider interaction among the various ions. The occurrence of such plants under sub-optimal conditions must be regarded as a result of competition with other species in those areas where the sodium chloride concentration is nearer their optimum. They do not grow in these places

nia marina was much lower than that of the parent tissue surrounding them and also of ordinary sea water. In passing from the seed coat to the seed there was a transition from a region of high to one of low osmotic pressure, and it was suggested that the necessary negative absorption pressure occurred in the cotyledonary haustoria. A physiological investigation should be able to show to what extent this hypothesis is correct. Complete seed-

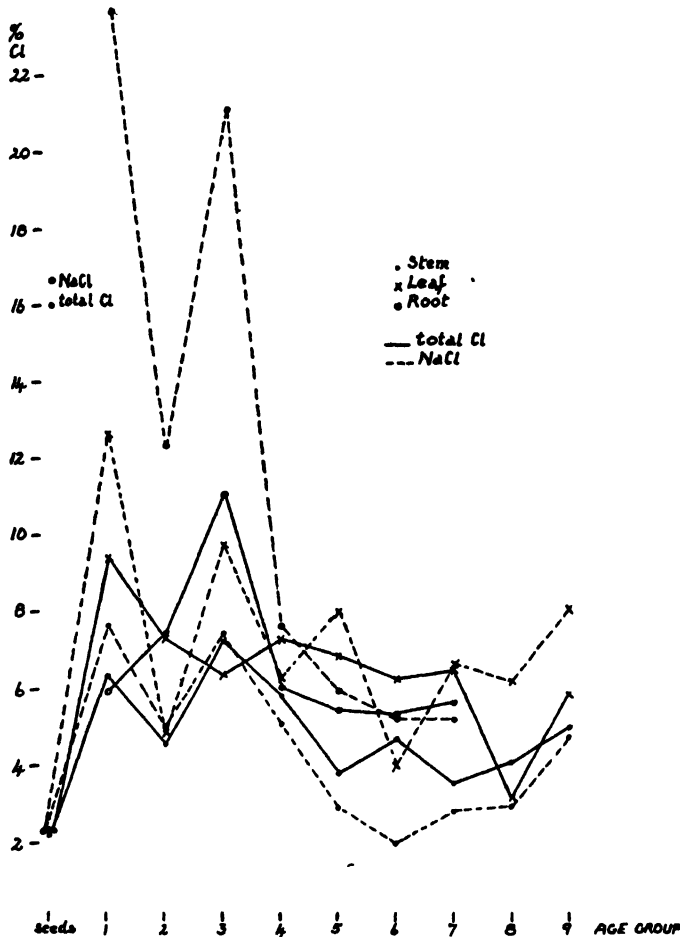


FIG. 10. CHANGES IN TOTAL CHLORIDE AND CHLORIDE ASSOCIATED WITH EXCHANGEABLE SODIUM IN A SERIES OF SEEDLINGS OF *LAGUNCULARIA RACEMOSA*

because the conditions are such that the other species are also able to flourish and dominate the vegetation.

There are still problems concerned with mangrove seedlings though these are to a large extent physiological rather than ecological. In 1936 Walter and Steiner discovered that the sodium chloride content of complete seedlings of *Rhizophora mucronata*, *Ceriops Candolleana* and *Avicen-*

lings and portions of seedlings of *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia nitida* were analyzed by the present writer and the same phenomenon observed. In the last two species there was a sharp rise in the Cl^- content in the tissues as soon as the seedling had fallen to the ground (Fig. 10). It may be suggested that the rate of absorption of the sodium chloride is very high in proportion to the total dry weight of the

plant while it is still young, and that the rate subsequently falls off, or else that later a mechanism develops which controls the absorption of the Na^+ and Cl^- ions. Such a mechanism might well be concerned with the development of the characteristic periderm, but here again we are in the realm of hypotheses. The vista is there but it can only be trod with the aid of a study in physiological anatomy.

VIII. ANATOMY

One cannot do more here than refer briefly to some of the numerous problems that still await attention. Many of the genera possess structures that are said to be either salt secreting glands or else hydathodes (*Statice*, *Glaux*, *Spartina*, *Limonium*, *Avicennia*). The morphology of these organs is well known, but the evidence for their function is far too often one of supposition or analogy, and it would be well if they could be subjected to experimental treatment. Another structure that offers considerable possibilities is the so-called lenticel hydathode which can be found in the leaves of *Avicennia nitida*. What stimulus is responsible for its development? What is its true function? What are the causal factors behind this type of periderm formation in leaf tissues? All these and a host of other questions leap to the mind. Further anatomical study may lead to some advance, but experiments along the paths laid down by Priestley in 1922 are more likely to yield the correct answers.

There is also the aerenchymatous tissue that is such a feature of many halophytes. We are beginning to understand a little about the development of aerenchyma, thanks to studies such as those of Sifton (1940) and McPherson (1939) on *Zea* and *Thea groenlandicum*. So far, however, no one has investigated experimentally the problem of aerenchyma in the halophytes. Is it associated with lack of calcium salts, inadequate oxygen supply or too high a percentage of water in the soil? Another problem is the development of cork in the pneumatophores of the mangrove genera *Brughiera*, *Sonneratia* and *Avicennia*. Here again more excellent material is available waiting to be used in an experimental investigation.

IX. AUTECOLOGY

Really adequate autecological studies of individual species are extremely rare; nevertheless no major advance in our knowledge of halophytic

vegetation will come until we are in a position to understand the life history, anatomy and reactions of individual species. This point was stressed in an earlier review (1936) and the need is still present. In 1936 I attempted to put together what was then known about *Salicornia herbacea* agg., though this was hardly satisfactory in view of the systematic confusion of the species. Since that time some work has been carried out on *Aster Tripolium* and *A. subulatus*, while we also know something about the biology of *Obione portulacoides*. The two halophytic species about which most is known are probably *Sonneratia alba* and *Avicennia nitida*. In both cases their morphological development has been studied and also their environment.

It has been shown (work now being prepared for publication) that *Avicennia nitida* can grow in a great variety of soils under a wide range of conditions; it is therefore an extremely tolerant species. It is largely on account of this tolerance that it occupies such extensive areas among the mangrove swamps of the New World. The available evidence suggests that the vertical distribution of the species on the shore is controlled primarily by the periods of non-tidal exposure (a period of two or more days during which no tide floods the area), together with indirect effects related to such periods, at the time of seedling establishment. We are not in a position to be quite so dogmatic about *Sonneratia*. While non-tidal exposure may account for the local occurrence and vertical range of *Avicennia*, J. H. Davis (1940) has pointed out that its geographical spread north and south is probably controlled by the incidence of killing frosts or of temperatures below 25°F .

In the case of *Obione portulacoides* we know very little about its seedling development, except that water-logging is inimical and that therefore it is commonly restricted to areas where drainage is good, e.g. along the banks of salt marsh creeks or on sandy marshes. Two varieties of this species are to be found in Great Britain, and their distribution is probably correlated with certain soil conditions. It is also possible that the northern limit of this species in Great Britain is related to the average monthly isotherms.

Aster Tripolium exists in Great Britain in two forms, a rayless variety, var. *discoideus*, and the normal plant with purple rays. The distribution of the rayless form is very restricted compared to that of the rayed as it appears only in southern

England and at Varel in Germany. The northern limit of the variety may be limited by the average monthly isotherms, though it is possible that it is still slowly spreading northwards. It has already been mentioned that the local occurrence of *Aster Tripolium* is controlled by the salinity of the soil surface in the spring when seed germination takes place. Once this species is established in a new area, however, further colonization takes place by disintegration of the clusters, the original rhizome commonly dying after two to three years. As the adult plant does not appear to be so sensitive to high salt concentrations it is able to invade areas other than that in which it started through vegetative propagation, and its spread to lower marshes by this means is probably controlled by the amount of submergence to which the plants are exposed rather than salinity. *Aster* also responds very remarkably to grazing—as may be seen from plants on grazed marshes.

One cannot work on salt marshes without appreciating one fact of major importance, namely, that certain conditions may be necessary for the establishment of the individual species, but once they have arrived in an area further spread takes place steadily by vegetative means, e.g. *Puccinellia maritima*, *Aster*, *Spartina*, *Triglochin*. In any autecological study we have to consider two groups of factors which can control spread: a) those controlling the appearance of the species and b) those determining its subsequent spread. Generally these may be expected to show some difference.

X. GENETICS AND DISTRIBUTION

Some halophytes would seem to form extremely valuable material for genetical studies in relation to environment and geographical distribution. A paper by Gregor (1939) on the maritime sea plantains and their related alpine forms emphasizes this point. Gregor has been able to show that the North American, Greenland and North European maritime species are all diploid and that they can be regarded as forming, together with the diploid alpine species, one inter-fertile group or ecospecies (by an ecospecies Gregor means a population with an inherently low capacity for exchanging genes with other populations of its coenospecies). This group stands in contrast to the tetraploid alpine species which form another inter-fertile group or ecospecies. In the diploid maritime species only one abrupt transition is found, namely, the North

American and Greenland forms are self compatible and typically have four seed capsules whereas the European plants are incompatible and have two seed capsules. In their other characters the so-called species overlap, although they frequently show a gradient related to (a) type of habitat in any region; (b) the transition from one geographical area to another (Fig. 11). The ecospecies may also be subdivided according to certain characters that occur locally. Iversen (1936) has pointed out that in ecospecies *Plantago maritima* on Danish marshes there are at least two varieties, vars. *subglabra* and *pilosa*. The former has a glabrous scape and grows on moist marsh soil and flowers during June and July, while the latter, which has a hairy

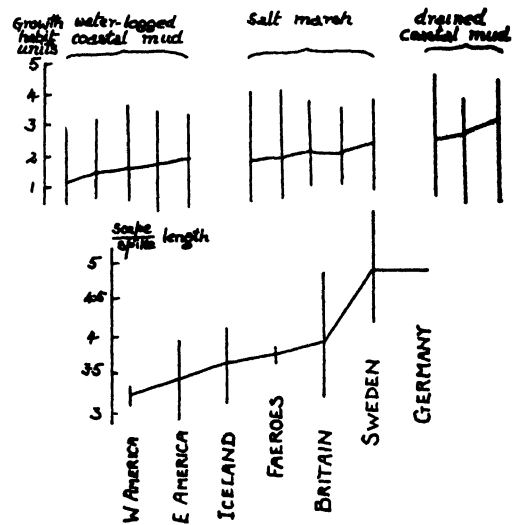


FIG. 11. GRADATION IN CERTAIN CHARACTERS AMONG THE MARITIME SEA PLANTAINS FROM DIFFERENT REGIONS OR TYPES OF HABITAT (After Gregor.)

scape, occurs on dry sandy soil and blooms from July to October. Iversen also noted that var. *subglabra* could be segregated into two forms: there was the normal plant which bloomed in July and there was also an early blooming *F. praecox* that flowered in June, and which, because of its premature flowering period, was not able to hybridize with var. *pilosa*. *Forma praecox* was also interesting because it grew in areas where marsh hay grass was cut, and it is possible that annual mowing has gradually selected out this early blooming form. Since marsh grass is cut in other parts of the world it would be of interest to ascertain whether there are other species which have responded similarly. *Armeria maritima*, for example; is a species which

might amply repay study in this respect since it is highly polymorphic and occurs on mountains and in salt marsh and other maritime habitats. Four varieties or races have already been distinguished; var. *maritima*, which has slightly fleshy leaves, var. *intermedia*, var. *elongata*, which is the alpine form, and var. *salina* from the Baltic. In Germany, Holland and Scandinavia segregation of these forms has taken place and each appears to possess a definite ecological significance. It would be well worth while studying this species in other countries where it occurs, employing for the purpose an extensive series of transplant experiments. Once again only the fringe of the problem has been investigated and an enormous field awaits the future investigator.

these two groups live under very different conditions, many of the species being restricted to either one or the other type. The segregation in the American marshes is not so obvious but more data would be desirable. Among the numerous subsidiary factors, which are related to the tidal movements, are the actual number of submergences per month, the hours submerged in daylight and the maximum periods of non-tidal exposure, this last item being of great importance depending on the time of year when it occurs. It is probable that each individual species living on a marsh is controlled to some extent by one or more of these factors, but until an attempt has been made to investigate their effects along experimental lines we shall not make much progress. So far, perhaps

TABLE 5
Analysis of tidal phenomena in swamp near Kingston, Jamaica

VEGETATION	LEVEL (ARBITRARY DATUM)	NUMBER OF SUBMERGENCES PER ANNUM	MONTH OF GREATEST SUBMERGENCE	MAXIMUM PERIOD OF NON-TIDAL EXPOSURE (Days)	SEASON OF MAXIMUM PERIOD OF NON-TIDAL EXPOSURE
<i>Laguncularia/Conocarpus</i> boundary.....	1.57'	4	October	339	November–September
Centre of salina.....	1.21'	150	October	125	December–March
<i>Avicennia/Laguncularia</i> boundary.....	1.14'	213	October	110	Mid-December–March
<i>Avicennia</i> swamp.....	0.84'	432	September	52	January–February
<i>Avicennia/Rhizophora</i> boundary.....	0.60'	524	August	10	January
<i>Rhizophora</i> swamp.....	Below 0.60'	530–700+	—	0–10	—

XI. TIDAL PHENOMENA

Although this is perhaps one of the major factors which operates where halophytic vegetation is to be found, it has deliberately been left to the end of this review because on the whole less is known about it than any other factor, and also it is so involved with subsidiary factors that it is well-nigh impossible to distinguish their effects. An analysis of the tidal factor has only been carried out for two sets of marshes in America (Johnson and York, 1915; Chapman, 1940), for one series in England (Chapman, 1938) and for some mangrove swamps in Jamaica (Chapman, in prep.). These analyses, however, have been sufficient to indicate some very important features, and it is highly desirable that this type of work should be extended to other areas. In England the salt marshes of Norfolk can be separated into two well-marked categories, the upper and the lower marshes, and the plants on

because of the magnitude of the problem and its complexity, no such attempt has been made. The problem in the mangrove swamps is of a slightly different nature because here submergence does not apply to the whole plant but only affects the roots and pneumatophores. One is apt to believe that most mangrove swamps are regularly inundated by the tide, but an actual analysis of the conditions produces results that are somewhat astonishing. Table 5 records the principal results of an analysis of the tidal phenomena in a swamp near Kingston, Jamaica.

Although the maximum tidal range is about one foot, a small rise or fall in level brings about profound changes in the number of submergences and in the maximum period of non-tidal exposure. The latter is particularly important, and it would seem evident that in the past insufficient attention has been paid to this factor, especially in its effect

on seedlings during the critical period of their establishment.

Apart from the effects of the tide upon the growth of the plants during their life there is also a mechanical effect which up to the present has only seriously been investigated for one species. Wiehe (1935) has shown that on the salt marshes of the Dovey, where the soil is sandy, the incidence of high tides during the first three days after germination may uproot a very high proportion of the *Salicornia* seedlings and hence seriously modify the annual distribution of the adult plants. Such an effect, of course, will only tend to operate in loose soils, i.e. soils with plenty of sand or shingle present or else composed of soft ooze. This mechanical effect is a feature that should be studied in mangrove swamps in relation to the distribution of the seeds and viviparous seedlings. The present author believes that it may have a significant effect upon the rate of colonization of an area by either *Avicennia nitida* or *Laguncularia racemosa*.

XII. CONCLUSIONS

The main purpose of this essay has been to summarize the more important recent contributions about the halophytes with the object of indicating the lines along which future development might be expected to be most profitable. The term 'halophyte' may be used in a general sense to include all plants which can tolerate more than 0.5 per cent sodium chloride, but those plants which are restricted to habitats where there is more than 0.5 per cent sodium chloride or whose optimal development takes place under such conditions should be termed 'euhalophytes.' The term 'miohalophyte' should be applied to those plants which are often found in haline habitats but whose optimal growth takes place under conditions where there is less than 0.5 per cent sodium chloride. Any plant which normally grows under glycophytic conditions but which nevertheless has some resistance to excess salt can be called a 'halo-glycophyte.'

The recent advances have been considerable and they demand radical changes in our future approach to the problems. In particular the effect of individual anions and cations on succulence, growth and transpiration mean that much of the past work will have to be repeated in the light of this new knowledge. There is also the differential adsorption of the ions in the various types of haline soils, about which remarkably little is known, while an associated phenomenon is the differential absorption of ions by the roots of the plants.

Here too an almost virgin field awaits the investigator. Much still remains to be solved concerning the regulatory mechanisms of osmotic pressures in the halophytes, especially in those species where there is apparently no controlling mechanism. One of the more urgent problems demanding attention is a study of the factors controlling establishment and development of the seedlings of halophytes, together with the biochemical changes that take place in the developing tissues in relation to the accumulation of salts. This is not only of importance on general ecological grounds but it is essential in any autecological study.

The relation of the halophytic vegetation to soil types and soil characters, both physical and chemical, is a subject upon which we are woefully ignorant; such indications as there are suggest that a detailed study of this feature would add very considerably, not only to our understanding of the local distribution of the different communities, but also to a more general appreciation of the different seres that are to be found around the coasts. There is still a serious gap due to a lack of adequate autecological studies, and it seems clearer than ever that there is little hope of any great advance until we study each individual species in detail. In the past the halophytic vegetation and the seral successions have often been regarded as forming a relatively simple problem because of the great influence ascribed to sodium chloride. We are slowly beginning to realize the falsity of this position, and that we are really dealing with a bewildering complex of factors which results in successions that are as complex as any in ecological literature.

One of the environmental factors that would certainly repay more detailed investigation is that of non-tidal exposure, and its effect upon the individual plants at different stages of their life history. There are still anatomical features that have been given causal explanations in the past without any experimental proof, and such a position cannot be tolerated today. The euhalophytes and miohalophytes form excellent material for the application of experimental methods towards the elucidation of the functions of distinct anatomical structures, together with the interaction of the factors that are responsible for their development.

Much of what has been said applies more particularly to those halophytes which grow in the sea or on or near the shore. There is still a considerable population which inhabits inland haline seas and deserts. Conditions here are very different

from those on the sea-shore, and such plants and communities will require independent study. At present there are numerous descriptions of such halophytic communities and their component spe-

cies, but hardly anything is known quantitatively about their environment.

I am much indebted to Mr. G. E. Briggs, F.R.S., for his stimulating advice and criticism.

LIST OF LITERATURE

- ARNOLD, A. 1936. Beiträge zur ökologischen und chemischen Analyse des Halophytenproblems. *Jahrb. wiss. Bot.*, 83: 105.
- BATALIN, A. 1886. Wirkung des Chlornatriums auf die Entwicklung von *Salicornia herbacea*. *Bull. Congr. intern. de Bot. et Hort. St. Petersbourg*.
- CHAPMAN, G. W. 1931. The cause of succulence in plants. *New Phytol.*, 30: 119.
- CHAPMAN, V. J. 1936. The halophyte problem in the light of recent investigations. *QUART. REV. BIOL.*, 11: 209.
- . 1937. Note on a dune drainage system. *Mem. and Proc. Manch. Lit. and Phil. Soc.*, 81: 77.
- . 1938. Studies in salt marsh ecology, I-III. *Journ. Ecology*, 26: 144.
- . 1939. Studies in salt marsh ecology, IV and V. *Journ. Ecology*, 27: 160.
- . 1940. Studies in salt marsh ecology, VI and VII. *Journ. Ecology*, 28: 118.
- . 1941. Studies in salt marsh ecology, VIII. *Journ. Ecology*, 29: 71.
- CHEMEZON, H. 1910. Recherches anatomiques sur les plantes littorales. *Ann. Sci. nat. Bot.* 9 sér. 12: 117.
- DAVIS, J. H. 1940. The ecology and geologic rôle of mangroves in Florida. *Publ. Carn. Inst. Wash.*, 517: 216.
- EIJK, M. VAN. 1939. Analyse der Wirkung des NaCl auf die Entwicklung, Sukkulenz und Transpiration bei *Salicornia herbacea*. *Rec. Trav. Bot. Neerland.*, 36: 561.
- GREGOR, J. W. 1939. Experimental taxonomy, IV. Population differentiation in North American and European sea plants allied to *Plantago maritima*. *New Phytol.*, 38: 293.
- HILL, T. G., and HANLEY, J. A. 1914. The structure and water content of shingle beaches. *Journ. Ecology*, 2: 21.
- HOLTERMANN, C. 1907. Der Einfluss des Klimas auf den Bau der Pflanzengewebe. *Leipzig*.
- IVERSEN, J. 1936. Biologische Pflanzentypen als Hilfsmittel in der Vegetationsforschung. *Mödel. Skilling-Lab.*, 4: 1.
- JOHNSON, D. S., and YORK, M. S. 1915. The relation of plants to tide levels. *Publ. Carn. Inst. Wash.*
- KEILER, B. 1925. Halophyten und Xerophyten Studien. *Journ. Ecology*, 13: 225.
- LESAGE, P. M. 1890. Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. *Rev. Gen. Bot.*, 2: 55, 106, 163.
- LUNDEGÅRDH, H. 1939. An electro-chemical theory of absorption and respiration. *Nature*, 143: 203.
- MCPHERSON, D. C. 1939. Cortical air spaces in the roots of *Zea Mays*. *New Phytol.*, 28: 190.
- MEVIUS, W. 1927. Kalzium-ion und Wurzelwachstum. *Jahrb. wiss. Bot.*, 56: 183.
- MONTFORT, C. 1926. Physiologische und pflanzengeographische Seesalzwirkungen. I. *Jahrb. wiss. Bot.*, 65: 502.
- . 1927. Über Halobiose und ihre Abstufung. *Flora*, 21: 433.
- MONTFORT, C., and BRANDRUP, W. 1927, 1928. Physiologische und pflanzengeographische Seesalzwirkungen II and III. *Jahrb. wiss. Bot.*, 66: 902; 67: 105.
- NEUWOHNER, W. 1938. Der tagliche Verlauf von Assimilation und Atmung bei einigen Halophyten. *Planta*, 28: 644.
- OLIVER, F. W. 1924, 1925. Blakeney Point Reports. *Trans. Norf. and Nor. Nat. Soc.*, 9: 717, and 10: 67.
- PEARSALL, W. H., and EWING, J. 1929. The relation of nitrogen metabolism to plant succulence. *Ann. Bot.*, 43: 27.
- PENFOUND, W. T., and HATHAWAY, E. S. 1938. Plant communities in the marsh lands of south-eastern Louisiana. *Ecol. Mono.* 8: 1.
- PENHALLOW, D. P. 1908. The marsh lands of the New England coast. *Trans. Roy. Soc. Can. Ser. III*, 1.
- PRIESTLY, J. H., and WOFFENDEN, L. M. 1922. Causal factors in cork formation. *New Phytol.*, 21: 252.
- PURER, E. R. 1942. *Ecol. Mono.*, 12: 81.
- SCHRAZ, E. 1934. Beiträge zur Biologie der Halophyten. 1. *Jahrb. wiss. Bot.*, 80: 112.
- . 1935. Beiträge zur Biologie der Halophyten 2. *Jahrb. wiss. Bot.*, 81: 59.
- SIFTON, H. B. 1940. Lysigenous air spaces in the leaf of Labrador tea. *New Phytol.*, 29: 75.
- STEINER, M. 1934. Zur Ökologie der Salzmarschen der Nordöstlichen Vereinigten Staaten von Nordamerika. *Jahrb. wiss. Bot.*, 81: 94.
- STEWART, F. C. 1935. The mineral nutrition of plants. *Ann. Rev. of Biochem.*, 4: 519.
- STOCKER, O. 1928. Das Halophytenproblem. *Erg. der Biol.*, 3: 265.
- UPHOF, J. C. TH. 1941. Halophytes. *Bot. Rev.*, 7: 1.
- WALTER, H., and STEINER, M. 1936. Die Ökologie der Ost-Afrikanischen Mangroven. *Zeit. Bot.*, 30: 65.
- WIEBE, P. O. 1935. A quantitative study of the influence of tide upon populations of *Salicornia europaea*. *Journ. Ecology*, 23: 323.



THE DETERMINATION OF THE CASTES OF SOCIAL INSECTS

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POLYMORPHISM in the social insects and the history of the search for its causes received masterly treatment by Wheeler in his book, *The Social Insects* (1928). Since then there have been several attempts at experimental solutions of the problems of caste determination. The data thus far obtained are meagre, however, and statistical in nature, and it is obvious that data derived from experiments on social insects under laboratory conditions are especially difficult to evaluate. Because the problems of caste determination are of general biological interest and far from being solved, there has been a tendency to present conclusions despite paucity of evidence, and some of these conclusions have passed into the literature, although later findings have not substantiated them. Nevertheless, considered apart from these conclusions, the evidence obtained during the period since 1928 has shown a consistent trend. Until recently Wheeler had remained neutral with regard to theories of caste determination. In 1937, however, he undertook the defense of a position which is not in line with the trend of recent evidence or opinion. The time seems ripe, therefore, for a survey of the subject.

The fifteen years since Wheeler's book have seen marked advances in appreciation of the nature of the problems involved in caste determination. It must be emphasized, however, that in so far as the ants and the termites are concerned, only a beginning has been made toward the solution of these problems. Indeed, I feel it necessary to emphasize that the published researches of this period, as well as my own unpublished results, serve most importantly to emphasize the difficulties involved, especially as to laboratory methods and the analysis and interpretation of results. Further advances will depend largely upon the development of adequate methods of culture, rigorous scientific controls, and the application of suitable methods in evaluating the type of data resulting from such experiments. According to Goetsch (1936), the ideal approach is through the use of isolated indi-

viduals, and no doubt every effort should be made in this direction. But it is indeed a question whether the method is a feasible one with social animals. The individuals of an insect society are so highly interdependent (Emerson, 1939a, b) that the attempt to maintain and study them in isolation involves many of the difficulties encountered in isolating the organs or the cells of complex individuals, and, in addition, some which we call psychological, for lack of a more revealing physiological term. For example, C. S. Lafleur tells me (*in litt.*) that many ants when kept in isolation exhibit symptoms of extreme nervous agitation and, unless given company, die very shortly, as a result of nervous disturbance. To such obstacles to the study of social insects must be added those arising from cannibalism, endemic and epidemic bacterial diseases, and attacks of mites and fungi. Finally, there are the difficulties encountered in attempting to control moisture for organisms extremely dependent upon such a control, but accustomed at the same time to relatively great diurnal and annual shifts in temperature and helpless individually, or even in small groups, to effect such control. Control of factors and evaluation of their influence on experimental results must be accomplished by the student of caste determination, at least in the termites, when he seeks to use isolated groups, let alone isolated individuals, as controls and experimentals. If these problems are to be solved, they must be approached with full realization of the difficulties to be surmounted.

The general problem presented by the polymorphism of the social insects is, of course, the nature of the mechanisms which function in each generation of each species to cause the offspring of the same parents to develop, in relatively constant numbers, into several different types of individuals which possess the special morphological features and behavior patterns characteristic of the particular castes in the particular species, features correlated with the performance of special functions in the communal life.

There is plenty of evidence from the effects of parasitism to indicate that the ants are capable of responding very strikingly to purely somatic influences (Wheeler, 1928). Instances of the effects of parasitism on the development of individual termites are relatively few, but these few are striking. For example, certain peculiar individuals in Philippine colonies of the common mound-building termite of the Malayan region, *Macrotermes gilvus*, were described by Silvestri (1926) who showed them to owe their special characteristics to the effects on their development of a parasitic fly larva which develops in the head of the infested termite. I had encountered these individuals earlier and had designated them in my notes as "X caste" because of their structural differences and especially because of their distinctive behavior. They are larger than any other apterous individuals and attract attention by their rapid nervous movements. For all their differences it seems improbable that anyone would feel the need of postulating a special genetic mechanism to account for them. Yet these fly-infested individuals reach a terminal stage characterized by fairly definite size and distinct structural and psychological features. If they were present in all colonies, and in relatively stable numbers, they would almost certainly be considered a special caste, especially so if they performed some special function in the colony. As it is, they are to be considered as anomalous forms, and fall outside the field of our discussion except as they may serve to indicate the enormous range of differences between individuals of the social insects which may result from the influence of non-genetic factors.

All modern students admit a genetic basis for the features of the different castes. The real problem is, therefore, whether the genetic factors determining the appearance of the different castes are segregated to certain individuals, which are thereby determined to become the particular caste, or whether, on the other hand, all individuals possess the complete genic complex, which would permit them to develop into any one of the castes (except in so far as sex determination is involved in the Hymenoptera).

It is obvious, of course, that the polymorphisms of orders so widely separated phylogenetically as are the Hymenoptera and the Isoptera (the termites) must be separate evolutionary achievements. Indeed, the arguments for separate origins of social habits in different groups of the Hymenop-

tera, the wasps, bees, and ants (Wheeler, 1928) are difficult to escape. Accepting the independent origin of polymorphism in wasps, bees, ants, and termites, it follows that findings with regard to one group have only the value of analogy when applied to the other. The argument from analogy does have its values, however (see Emerson, 1939a, p. 199), particularly when the proven facts with regard to some of the groups agree with the trend of the evidence in the others, as will be seen to be the case.

CASTES IN THE SOCIAL HYMENOPTERA

Social habits have originated several times among the wasps and bees and many species of each group are still solitary. The social habits of the ants are much more ancient than those of the wasps and bees and have undergone a multifarious evolution within the group (Wheeler, 1928, p. 173). Ants are all social and it must be supposed that they derive from a social ancestral stock.

Determination of the castes of the social Hymenoptera obviously includes two sharply distinct sets of problems. On the one hand are the problems arising out of the strong differences between the two reproductive castes, problems tied up, therefore, with sex determination. On the other hand are the very different problems which arise from the universal occurrence of distinct sterile castes, all individuals of which are female.

DETERMINATION OF THE REPRODUCTIVE CASTES

Strikingly different in structure, behavior, and rôle in the colony, the reproductively functional individuals of the two sexes of the social Hymenoptera have always been considered to constitute distinct castes. Here, as in most animals, the sexual dimorphism has a genetic basis. Further, it is typically associated here, as in other Hymenoptera, with major differences in the chromosomal complement, the males being haploid, the females typically diploid.

That male honeybees develop from unfertilized eggs, and females (queens and workers) from fertilized eggs, was first stated by Dzierzon (1845) and long defended by him, and has come to be known as Dzierzon's Law or Rule (see Wheeler, 1923, p. 139, and Whiting, 1935, p. 263). More recently there have been demonstrated structural mechanisms controlling the emission of spermatozoa from the spermatheca (see Snodgrass, 1925; Flanders, 1939).

Flanders (p. 13) says, "So far as we know at present, the control of fertilization in the honeybee depends upon the 'will' of the queen as asserted in 1845 by Dzierzon." Flanders concludes, however, that "the sex ratio of the eggs deposited by arrhenotokous species appears to be largely externally induced" and that in the case of the honeybee it is determined by the size of the available cells, drone cells being larger than other brood cells at the time the eggs are laid. In the parasitic Hymenoptera the sex ratio has been shown in several instances to depend upon external factors. For example, eggs laid by numerous parasites in hosts of optimum size are predominantly fertilized, whereas those laid in small hosts are predominantly unfertilized, and Flanders tells me (*in litt.*) that *Coccophagus ochraceus* "deposits diploid eggs in the body fluid of the black scale and haploid eggs out side of the body of the black scale." (For references and discussion see Flanders, 1939.)

The literature abounds in seeming exceptions to Dzierzon's Law. However, Goetsch and Käthner (1937), after summing up the evidence for the ants, state that without exception unfertilized eggs of worker ants and eggs of virgin queens give rise to males, and Whiting (1935) says that there is no evidence of males of wild species arising from fertilized eggs in the Hymenoptera thus far studied. True biparental males are reported to occur, however, in domestic and laboratory stocks (Whiting, 1935).

Some at least of the occurrences of seemingly uniparental females in the social Hymenoptera are known to be due to the fact that many egg-laying workers formerly assumed to be virgin are actually inseminated (Goetsch and Käthner, 1937).

Further indications of complexity in the genetic mechanisms concerned in sex determination in Hymenoptera derive from the common occurrence of sex intergrades and sex mosaics (Wheeler, 1928; Whiting, 1938). Bridges (1925, p. 134) pointed out that the mere doubling of chromosomes in the female could not account for female determination, and sex determination in the Hymenoptera is now explained on the basis of female heterozygosity and the action of a series of multiple sex alleles (Whiting, 1933, 1935, 1939, 1940; Bostian, 1939). Most of the work has been done by Whiting and his students, using the parasitic wasp *Habrobracon*, but it seems probable that similar conditions will be found to occur widely among the Hymenoptera. To explain the absence or very low incidence of

biparental males, Whiting (1935) mentioned their low viability and tentatively suggested a theory of differential maturation to explain genetic results. The same year Snell suggested that femaleness results from heterozygosity with regard to one or more of a number of sex factors on different chromosomes, and pointed out that the chance of unrelated parents giving diploid males would be very slight if there were five independently segregating pairs of such sex determining genes.

Whiting (1939) proposed the theory of multiple alleles on the basis of the behavior of the gene *fused*. Introduced into two stocks having different sex factors, *fused* proved to be similarly linked with the sex gene, proving that these sex factors must be in a single series (at the same locus of the same chromosome). Bostian (1939) reported data indicating three members in a series of sex alleles thus showing Snell's hypothesis to be very improbable. Whiting (1940) reviewed the whole problem and later (1941) presented proof of a fourth member. He tells me (*in litt.*) that he now has proof of nine members of the series in his stock, and believes that others exist in wild strains. According to this theory (Whiting, 1940a, p. 333), "Any heterozygote is a female, any homozygote or azygote (haploid) a male." Biparental males are absent in crosses between unrelated strains (outcrosses) since the sex allele of the male is different from either sex allele of the female. In closecrosses of related strains their occurrence varies, but is usually low. The low incidence in closecrosses is explained by low viability, which is in turn affected by "diverse factors, both genetic and environmental" (Whiting, 1940, p. 354).

Whiting points out (*in litt.*) that the work of Speicher and of Inaba on other species of *Habrobracon* indicates that "the same principles probably apply to these forms" and that Dozorzeva's work on *Pteromalus puparum* "shows that widely diverse branches of the order act similarly." In this connection it is interesting to note that Flanders, who has worked on the sex ratio of several parasitic species (1939, 1942a, b), says (*in litt.*) that he believes the diploid males obtained by Whiting are abnormal and probably due to sex reversal.

DETERMINATION OF THE DIFFERENT FEMALE CASTES

Determination of the two sexes and therefore of the two reproductive castes, as shown above, derives from genetic differences in the egg and is in accord, therefore, with the blastogenic theory (in

modern terminology, the genetic theory) of caste determination stemming from Weismann and upheld for the ants by Forel and, latterly (1937), by Wheeler. The differentiation of the two female castes presents, on the contrary, in the wasps and bees at least, an equally convincing case for control by extrinsic factors, in this case nutritional factors, in accord with the somatogenic, specifically the trophogenic, theory of caste determination as upheld by a long series of students, notably Wasmann and Emery.

The worker caste is poorly developed in most wasps. In ontogenetic development the first non-reproductive females (the only ones of many species) are sterile because of an adult starvation resulting from giving their food to the numerous larvae. Later in the same colony sterility results from alimentary castration, the larvae receiving minimal amounts of food and developing into small, sexually undeveloped worker adults (Wheeler, 1928, p. 167). Marchal (1896, 1897) found that elimination of the queen from a *Vespa* colony resulted in development of functional sexuality (egg-laying) by one-third of the brood, relieved under these conditions from nursing duties. He found that permanent or even temporary suppression of egg laying by the queen gave similar results.

"The differences between the workers and the queens of wasps are so small and intermediate forms are so numerous that quantitative feeding would probably account for their production. The normal sterility of the workers seems to be due to the acceleration of the somatic and retardation of the reproductive tissues, a condition the reverse of neotenia" (Wheeler, 1928, p. 196).

Caste development in the humblebees seems to be on the same basis as that of the wasps. In the stingless bees and the honeybee, however, the differences between queen and worker castes are exaggerated. The morphological specialization of the worker is more advanced, and the queens show numerous degenerative features. The queens of these societies, it must be remembered, are parasitic in a sense, entirely dependent on the workers and not functional in colony activities except as reproductives. The difference between queens and workers in the social bees then is by no means merely a matter of sex repression.

The method of determination of the distinct female castes is best known for the honeybee,

although seemingly many points remain to be cleared up even here. The essential facts have long been known. Eggs laid in queen cells become queens, those in worker cells become workers. All young larvae receive the same food up until the middle of the third day. Queens receive the secretion of the pharyngeal gland known as royal jelly throughout larval life. The larvae in worker cells

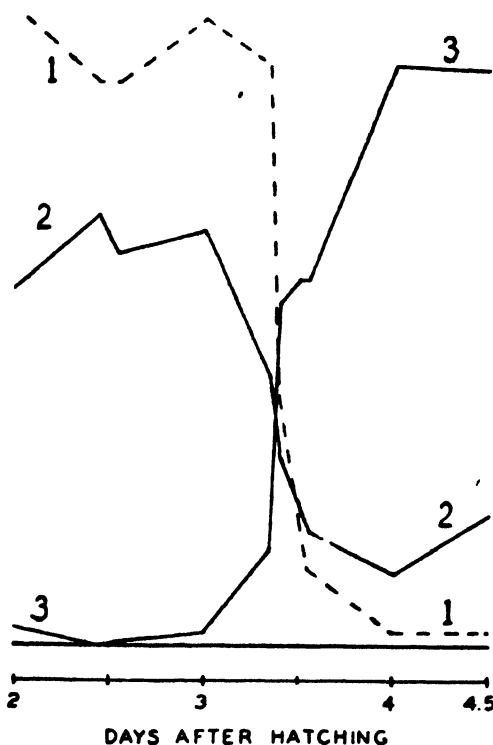


FIG. 1. SCHEMATIC REPRESENTATION OF SOME OF THE MAJOR CHANGES WHICH OCCUR IN THE DEVELOPMENT OF FEMALE LARVAE OF THE HONEYBEE IN WORKER CELLS DURING THE THIRD AND FOURTH DAYS OF DEVELOPMENT, FOLLOWING THE ADDITION OF POLLEN TO THE DIET. (FROM FIG. 24 OF BECKER, 1925)

1. Decrease in number of ovarian tubules. 2. Decrease in size of mandibular gland. 3. Increase in size of pharyngeal gland.

receive pollen in increasing amounts beginning from about the middle of the third day. Becker (1925, in Zander and Becker, p. 215) showed (Fig. 1) that sudden and striking change in direction and rate of development of the features in which workers differed from queens coincides with the first feeding with pollen. Up to this point any female larva seems capable of becoming either a queen or a worker, as has been shown by transfer-

ring eggs from worker cells to queen cells, and vice versa (Wheeler, 1923, p. 137). Furthermore, numerous intermediates have been produced by transferring worker larvae to queen cells at various times beyond the second and third days of larval life. Becker states that the queen and the worker are the extremes of a morphological series, the intermediates of which may be experimentally produced by varying the food. It should be noted that the queen emerges much earlier than does the worker. This early emergence may be correlated with access to greater quantity and richer quality of food, but also perhaps with the fact that certain structures do not reach full development.

Instead of feeding the growing larvae as does the honeybee, the stingless bees (*Meliponinae*), like the solitary bees, seal the brood cells, each containing an egg and food for the growth of the future larva. In some *Meliponinae*, queen cells are larger than worker cells. Here the mere quantitative differences in food supply may be responsible for the differences between queens and workers. In the species of the genus *Melipona*, however, it has long been known (Silvestri, 1902; H. von Ihering, 1903; Wheeler, 1928) that the cells are not distinguishably different in size, and Salt (1929, p. 435) says, "By opening many adjacent cells containing adult or nearly adult bees it was readily established that males, females, and workers occur in neighboring and similar cells indiscriminately mixed in the tiers." Wheeler (1928, p. 197) says of *Melipona*, "... the cells in which males, queens and workers are reared are all alike and of the same size. They are provisioned with the same kind of food, pollen and honey, and an egg is laid in each ... their uniform treatment nevertheless results in the production of two sharply differentiated female castes." If it should be shown that all brood cells contain the same food substances in the same proportions, we would have here inescapable proof of intrinsic differences in the eggs and, therefore, of the blastogenic theory. In the absence of evidence one can only predict in the light of conditions known to exist in the honeybee that further investigations will show that the food stored in cells in which queens develop is significantly different from that in cells in which workers develop.

DETERMINATIONS OF FEMALE CASTES IN ANTS

A consideration of female polymorphism in ants presents problems more complex and difficult and much farther from solution than is the case with

the bees and wasps. The situation was admirably described by Wheeler (1937, p. 39) as follows.

"It must be admitted that the brood relationship in ants is so elaborate, the difficulties of submitting it to controlled experimental investigation so great, and observations of it so conducive to conflicting 'explanations' that the controversy concerning the determination of castes in these insects has persisted with little change for many years. This is shown by the attitudes of the two very eminent myrmecologists, Emery and Forel. Although both were thoroughly conversant with all the relevant facts established during their lifetimes, Emery nevertheless remained an intransigent trophogenist throughout his career, and Forel ... was as thoroughly convinced that the castes are determined in the egg. During the past thirty years I have remained 'on the fence' on this controversy, with an increasing inclination to drop off on the blastogenic side."

In *Mosaics and Other Anomalies Among Ants* (1937), the last work before his death, Wheeler did definitely espouse the blastogenic theory (see quotation in preceding paragraph). He was led to this position by a study of the very numerous anomalies in a colony of the fungus-growing ant, *Acromyrmex octospinosus* Reich, collected in Trinidad by Dr. Albert Neal Weber, and studied by Weber there for three months in a laboratory observation colony. Wheeler believed these anomalies could only be explained as intercaste mosaics and therefore genetically determined as sex mosaics are known to be. Whiting (1938) in an extensive review of Wheeler's book showed that these and other ant anomalies could be interpreted as intercastes resulting from unusual and variable conditions as to nutrition or other environmental factors or as intersexes. Most importantly he points out that whereas the anomalous areas are distributed more or less at random in mosaics, the anomalies of ants tend to be limited to the head. Of the two other reviewers, one (Gregg, 1938) is also in disagreement with Wheeler's conclusions, and the other (Schmieder, 1938) feels that experimental evidence is still required to prove the blastogenic theory.

Two major sets of problems are involved in the female polymorphism of ants: first, those concerned with the determination of sterile versus fertile females, already discussed for bees and wasps, and, second, those dealing with the differentiation among the sterile individuals of distinct types known respectively as soldiers and workers.

First, then, the question already encountered in

the wasps and bees: Are the reproductive females on the one hand and the sterile castes on the other genetic segregants, or do they represent phenotypic extremes of a varying expression of the same genotype, their appearance determined by somatic influences? These are the two extremes of blastogenic versus somatogenic positions. A somewhat different somatogenic explanation would hold the existence of different genetic mechanisms for all female castes in all female-producing eggs, and postulate somatic (probably nutritional) factors which determine which of these genetic mechanisms shall function during the critical period of larval development.

In wasps, completely intergrading ontogenetic series exist between workers and queens, and in the honeybee such can be experimentally produced by variations in the diet. The presumption would be that such was once the case in ants. However, the polymorphism of ants is a much more ancient, much deeper-seated affair than in the other social Hymenoptera, and much more protean in its present-day expression. Individuals which are intermediate as to some characters between the queen and sterile workers occur naturally in some species, chiefly parasitic species, and such have been found to occur also when the natural development of individuals or the normal care of the brood is disturbed, as in various types and relations of parasitism. Whether the individuals thus caused to deviate from the normal of one or the other female castes actually form connecting series between queens on the one hand and a sterile caste on the other is a matter of opinion.

An extensive literature deals with the structural and psychological effects of infection of individual ants with nematodes of the genus *Mermis*. As late as 1928 Wheeler says (p. 206), "But whatever interpretation we adopt, the blending of characters of all three castes in the adult mermithergate seems clearly to point to potentialities for all of them in the young larvae." In 1937, influenced by the findings and arguments of Vandel (1930), and perhaps not entirely free from the influence of his own recent conversion to the blastogenic position, Wheeler says (1937, p. 77), "The character of the modification manifested by the adult ant depends therefore, on the caste of the infected larva," and he speaks of the trophogenic explanation of these anomalies given by him in 1928 as being "untenable."

The rich terminology of caste anomalies among the ants need not concern us here (see Wheeler,

1937, Appendix B, for his latest formulation, dictated by acceptance of the blastogenic position). Our consideration may be limited to those anomalous females known as pseudogynes, long studied by Wasmann and others. Their occurrence is definitely correlated in several ant genera with infestations of staphylinid beetles of several genera, chiefly *Lomechusa*, as shown by Wasmann in numerous papers, and by Viehmeyer (see Wheeler, 1928). The workers of infested colonies nurse the beetle larvae, neglecting the larvae of the colony. The appearance of anomalies, especially pseudogynes, under these circumstances was explained by the trophogenists as being due to irregularities in feeding the larvae. It should be noted that the appearance of pseudogynes persists long after the infestation has ended. This is explained by the trophogenists as due to continued irregularity in the behavior of the workers. It must be noted, also, that pseudogynes occur, also, in certain species "never parasitized by beetles" (Wheeler, 1937, p. 79), which allows the blastogenist to attribute their occurrence to irregularities in the eggs rather than to nutritional irregularities. In 1904 Viehmeyer obtained what he considers conclusive evidence (see also Viehmeyer, 1924) that these anomalies proceed not from irregularities in the eggs but from nutritional aberrations. A colony formerly infested with *Lomechusa* had produced pseudogynes for three successive years after cessation of the infestation. He transferred the queen of this colony to a group of workers from another colony which had never produced a pseudogyne. Under the care of these workers all of the eggs of this queen gave rise to normal individuals, none to pseudogynes. However, since we do not know all the causes of pseudogyne formation, Viehmeyer's results would have been much more conclusive had eggs produced by the transferred queen in the new colony been returned to the old colony as a control to demonstrate that they could still give rise to pseudogynes there. Even then the bearing on our question of these findings might be oblique, since pseudogynes are interpreted by Wheeler as abortive females (queens) and not as intermediates between the fertile and sterile female castes.

Various other types interpreted as intermediates between queens and workers are known to occur (Wheeler, 1928, p. 209; 1937, Appendix B). Some of these occur sporadically and are clearly abnormalities. Others, especially in the genus *Leptothorax*, are functional females, but "grading down from the winged queen to the smallest worker"

(Wheeler, 1928, p. 209). In 1937, however, he says (p. 62), speaking of *Leptothorax* again,

Besides the sudden absence of the wings in the ergatogynes, there is also a perceptible gap in thoracic structure The series seems, in fact, to comprise two series, one of females, with loss of wings and increasing simplification of the thorax, the other of workers, which increase in size and acquire ocelli . . . the semblance of a single graduated series seems to be produced by a recessive structural simplification of the females and a progressive increase in size and ovarian development (feminization) of the workers.

Ezhikov (1934), in an interesting statistical and theoretical discussion of individual variation and dimorphism of social insects, reports, without presentation of data, the general result of attempts to produce intermediates between workers and queens by quantitatively differential feeding: "When we subjected to hunger the larvae of ants destined to be females (*Camponotus*, *Myrmica*) at different moments of their development, we never were able to obtain forms transitional between the queen and the worker, but either real fertile females, perhaps somewhat reduced in size, or else typical working individuals."

Wesson (1940), approaching the same problem somewhat differently, attempted to show the effectiveness of environmental factors in shifting the proportions of queens produced from given numbers of female larvae. The young larvae from several colonies of *Leptothorax curvispinosus* were thoroughly mixed and introduced into a colony of *L. longispinosus* from which the queen and the brood had been removed. During two weeks at summer temperature, 32 per cent of the larvae disappeared and those persisting grew but little. Evidently there was incompatibility between brood and recipient workers. The mixed colony was then placed in the cold room at 2° C until March (five months later). On removal from the cold room another 33 per cent of smaller shriveled larvae was discarded and the remainder were thoroughly mixed again and the pile divided "into halves through the center." The host colony was divided into halves and each placed with one lot of the larvae. Colony A, consisting of 27 *longispinosus* workers and 44 *curvispinosus* larvae was given a superabundance of food. Colony B, consisting of 30 workers and 44 larvae, was given the same kind of food but just enough to allow the larvae to grow. Conditions otherwise were the same. The 38 larvae surviving to maturity in

colony A gave rise to 3 males, 32 queens and 3 workers, whereas the 35 surviving in the starved colony gave rise to 2 males, 23 workers and only 10 queens. These results are interesting but are so meagre as to make it unwise to base generalizations upon them. As Wesson says, they could conceivably be explained upon the basis of chance assortment. Further, it would be extremely valuable in estimating the significance of these differences to have information as to the numbers of each caste developed from such larvae in colonies of the donor species under normal conditions and also after removal of queen and brood both during the summer and in the spring. Further, one would suspect that the adoption of the foreign brood could have been accomplished by brief refrigeration alone, and that the artificial hibernation was not the important factor. One wonders, also, as to the 65 per cent of larvae lost. Perhaps here, as in the case of laboratory groups of termites, wide differences which seem to be of experimental significance may rest rather in variations of unknown complex social and environmental factors whose results are expressed in great differences in viability. However that may be, this is an excellent beginning and it is from such experiments more elaborately controlled and involving larger numbers of individuals and colonies that valuable results may be expected.

Except for a few parasitic genera, in which, supposedly, it has been secondarily lost, all ants possess a sharply defined worker caste. In the primitive subfamilies of ants the workers are large and monomorphic (Wheeler, 1923), although sometimes of different sizes. In many species in each of the higher subfamilies the sterile females exhibit polymorphism which may take the form of a more or less completely intergrading series or may be a sharply defined dimorphism. In the latter instance the large sterile type is termed the soldier and the smaller type the worker. These two types appear regularly in each colony of such ants and have very different functions in the economy of the colony. They are, in other words, well-defined castes in the proper use of the term. Here, therefore, the question arises as to the mechanism which determines their occurrence. Two recent attempts at an experimental solution of this problem are of interest.

Goetsch reports, in the brief accounts available to me (1937a, b), what seem to be significant findings as to the effects of diet on soldier production in colonies of the Italian house ant (*Pheidole*

pallidula). This species is especially favorable for such studies because of the ease with which incipient colonies may be cultured and because of the rapidity of its colony development. The first nanitic worker lives only two to four weeks but by that time the second series of workers is present. These second workers are usually of normal size for workers of this species and in such colonies the first soldier is also present. Thus there is presented here somewhat the same opportunity for study of the factors concerned in soldier production in ants as is furnished for termites by the incipient colony of *Zootermopsis*, to be discussed later.

All of the 26 colonies which produced soldiers were colonies which (1) contained larvae not older than 5 days when experimental feeding was begun and which (2) were fed solid proteinaceous foods. Only one colony in this category failed to produce soldiers. None of those whose larvae were older than 5 days produced soldiers, and none was produced in 18 colonies with young larvae but fed syrup or solid sugar or even fluid protein. Six of 8 such colonies fed syrup together with solid protein food produced soldiers, and one fed syrup but given a single piece of animal food produced a soldier-worker intermediate. Goetsch (1937a, p. 15) concludes, evidently partly on data not quantitatively presented in the reference available to me, "Es ist also lediglich eine Spanne von höchstens 2 Tagen, in der über das Schicksal der Larven bestimmt wird. Bekamen sie während dieser Zeit Fliegen- oder Mehlwurmstückchen, dann wuchsen sie zu Riesenlarven und später zu grossköpfigen Soldaten heran; im anderen Falle blieben sie Arbeiter!" Such of his results as are presented in the brief report available to me are recombined in Table 1. As presented, they seem to indicate the significance of diet in determining the soldier caste. The argument is more compelling when one notes that the six colonies which did produce soldiers (and for which information is given for numbers of soldiers) produced 21 of them, which would seem to make truly significant their total absence in the 16 similar colonies otherwise fed. Striking as these results seem at first glance, more careful consideration raises numerous questions. First, it will be noted that the factor involved is not entirely clear. It is not just the chemical nature of the food, apparently, since, although colonies fed solid protein produced soldiers, those fed liquid protein (blood, expressed tissue juices, raw egg white) or those starved (but supposedly fed proteinaceous food) did not. This, Goetsch thinks, may be

because the fluid materials had to be taken into the crop of the worker and fed to the larvae, whereas the solid protein food can be fed on continuously by the larvae; in other words, that it is a matter of quantity in the case of liquid proteins at least, as presumably also in the case of starvation. It should be remembered in evaluating these results that pieces of insect bodies are the normal food of the larvae of the species. From this point of view the findings seem less significant: Colonies with plenty of their normal food produced soldiers as well as workers whereas those receiving small

TABLE 1

*Summary of results of experiments by Goetsch (1937) on the influence of food on soldier development in colonies of *Pheidole pallidula**

FOOD	AGE	NUMBER OF COLONIES	NUMBER PRODUCING SOLDIERS
Flesh.....	Young*	22	22
Flesh.....	Old	3	0
Solid protein.....	Young	5	4
Flesh and syrup.....	Young	8	6
Syrup and one piece of flesh.....	Young	1	1**
Fluid protein.....	Young	4	0
Fluid protein.....	Old	1	0
Tissue juice.....	Young	2	0
Syrup.....	Young	5	0
Solid sugar.....	Young	7	0
Solid sugar.....	Old	2	0
Starved.....	Young	8	0

* All larvae designated as young were less than 5 days old.

** Intermediate between worker and soldier.

quantities of the normal food, or the normal type of food but in a different (less available) form, or other types of food, produced only workers. As Gregg (1942) says, the better-fed colony would be expected to produce soldiers. Soldiers always appear later than workers in the development of ant colonies and are larger, and their appearance would seem to depend upon abundant food supplies. The factor actually determining that one larva shall become a soldier, another a worker, remains obscure, however. Finally, data as to the complete brood of these colonies as also as to mortality in the colonies which did not produce soldiers would have been of interest in evaluating these results. These data may be given in other articles not seen by me.

In the same paper (1937), Goetsch reports on the nanism of the first worker. This he shows to be due to conditions in the egg, since eggs of young queens transferred to old colonies still give rise to nanitic workers. He considers nanism as an example of blastogenic determination, although he clearly considers it a matter of quantity of food available during embryonic development. Certainly there is no reason to think that these eggs are genetically different from the others. The time would seem to have come to discard the term blastogenic, unless it can be used in conformity with modern genetic usages. Its use otherwise can only lead to misunderstanding.

Most recently Gregg (1942) presents the results of a most interesting attempt to determine the significance of the constitution of the colony in determining the proportion of soldiers or workers produced within a colony. *Pheidole morrisi* was chosen because it is dimorphic as to sterile castes and because its soldiers are able to care for the brood. Numerous experimental colonies of varying sizes were set up. Seventeen were composed, aside from the queen, nearly or entirely of workers, 10 nearly or entirely of soldiers, and 6, as controls, of workers and soldiers as taken in the field. In the 6 control colonies, soldiers produced ranged from 0 to 17.5 per cent of the brood with an average of 7.3 per cent. In the 17 worker colonies, caste production was not strikingly different from that in the controls. Soldier production ranged from 0 to 18.6 per cent of the brood in 16 colonies and was 46.5 per cent in one colony, the average being 8.5 per cent. In the 10 soldier colonies, on the contrary, soldier production was very low, 0 in 4 of them and from 0.5 to 1 per cent in the others. One possible explanation of these results is that soldiers are not as effective as nurses as are workers and that almost all individuals in the colonies developed, therefore, under suboptimal conditions and became workers instead of soldiers, for the same reasons as in a young or undernourished colony. As Gregg points out, the soldiers did not appear in most cases until after there were numerous workers in the colony. The number which did appear is so small, however, as to weaken the significance of the time of their appearance. However this may be, Gregg's excellent study adds to the growing evidence for the theory that any young female larva is capable of producing any of the female castes, depending on the conditions at critical moments of development. The same may be

said, of course, of the findings of Wesson and of Goetsch.

Gregg's results indicated a tendency toward regulation of the colonies experimentally altered as to caste composition to something approximating the statistically normal proportion of soldiers. From the data given by Gregg, it appears that while the ratio between workers and soldiers varies enormously in individual colonies in nature, the average proportion of workers seems fairly definite, both for the species used by him and for the other species of the genus *Pheidole* investigated by him. His 6 control colonies averaged 86 per cent workers at the end of the experiment, 16 other colonies of the same species averaged 81.9 per cent workers, and a somewhat similar figure was found for 29 colonies of *Pheidole bicarinata* (89.24 per cent) and for *P. pilifera* (88.5 per cent). A shift in composition of the worker colonies would result naturally from the fact that soldiers were produced in considerable numbers. Actually a somewhat larger number of soldiers was produced in them (an average of 8.5 per cent) than was produced in the control colonies (7.3 per cent). If this increased soldier production in worker colonies is significant it may be explained on the basis of the optimal conditions found in these well-fed colonies with plenty of workers. An alternate hypothesis would be that more soldiers were produced because of freedom from an inhibiting effect exerted by soldiers. The shift toward normal composition in the soldier colonies occurred, of course, because, while almost no soldiers were produced, numerous workers were. The lack of soldier production here may be explained, as noted above, as being due in part at least to the unfavorable conditions arising from the absence of workers, or as Gregg postulates, as being a direct result of inhibition arising from the presence of numerous soldiers.

Perusal of Gregg's figures reveals that the size of the brood produced by different colonies varied greatly. If we ignore two small colonies which died out, the range in size of brood produced for his worker colonies is seen to be 122 to 1135. Further, of the two largest broods produced by his worker colonies one was produced by a colony starting with 60 workers, the other by one starting with 2,008 workers. Perhaps no correlation between size of colony and size of brood is to be expected. Even so, the discrepancies in size of brood remain unexplained.

Finally, such data as are given indicate that

there was a very high mortality during the experiment and that the incidence of mortality by colonies was by no means consistent. These are situations all too familiar to the laboratory student of termites and suggest the existence of undefined variables affecting the results. I present these features of Gregg's results not as criticisms but to emphasize the necessity for great caution in evaluating the data derived from laboratory studies of social insects under existing laboratory methods.

DETERMINATION OF CASTES IN TERMITES

Smethman's remarkably accurate account of the colonies and communal structures of tropical termites (1778) gave the first clear picture of the facts of polymorphism and social organization in the termites. For more than another century, however, the study of the termite castes remained in the observational and speculative stage. During this period the most noteworthy contributions were those of Lespes (1856) and Fritz Müller (1873 *et seq.*). Grassi's classic studies (Grassi and Sandias, 1893, 1894; English translation, 1897, 1898) furnished the first experimental results and laid an excellent basis for future studies. In the half century since then numerous students have attacked the problems of caste determination and an extensive literature has arisen.

Here, as with the ants, two theories have long been in opposition. The so-called blastogenic theory holds that the different castes appear as a result of intrinsic, that is genetic, differences in the eggs (Bugnion, 1912a, 1913; Imms, 1919; Thompson, 1917, 1919, 1922; Thompson and Snyder, 1919, 1920; Snyder, 1925, 1926; Bathellier, 1927). The somatogenic theory, on the other hand, holds that all eggs and early nymphs are alike and that their ultimate fate is determined by environmental influences (Grassi and Sandias; Heath, 1927, 1931; Kalshoven, 1930; Weyer, 1930, 1931; Pickens, 1932, 1934; Castle, 1934a, b; Hare, 1934; Goetsch, 1936, 1939; Miller, 1942). In addition, important contributions have been made by Emerson (1926, 1939a, b) and Adamson (1940).

The blastogenic theory received factual support from two sources. First, Bugnion (1912, 1913) reported finding newly hatched nymphs (larvae in European usage) of a nasute species in which the nasus of the soldier was already differentiated. This report was discredited by Thompson (1919) on the basis of earlier work by Knowler (1894) and her own findings, and also by John (1925), who

reinvestigated the species studied by Bugnion. Second was the seemingly careful work of Thompson (1917, 1919, 1922) in which she presented what appeared to be convincing evidence that in each of nine different genera of termites from three different families the nymphs of the first instar included two types of individuals, and that these types represented, respectively, those nymphs destined to develop into reproductives and those determined as sterile individuals.

The studies of Heath (1927) showed that Thompson's supposed types were not discernible in first-instar nymphs of *Zootermopsis* (formerly *Termopsis*). Weyer (1931) showed that the first-instar nymphs ("larvae") of three species of higher termites gave indications of a normal distribution of variation with regard to size of brain and head instead of falling into two types, and pointed out further that Thompson's data could not be properly evaluated, since no information was given as to the numbers of individuals measured nor the distribution of the different measurements. For these reasons he emphasized the necessity of completely disregarding both her evidence and any generalizations based on it.

Finally, Hare (1934), working with three American species of *Reticulitermes*, including the species studied by Thompson, and having access to the actual specimens studied by Thompson, concludes (1) that Thompson's supposed first stadium actually covered the first three stadia, (2) that within the true first instar the frequency scale of head width to brain width approximates a unimodal curve, (3) that there is little if any correlation between large gonad and small head-brain ratios, or vice versa, and (4) that not until a late stadium when certain individuals show wing buds can the nymphs of the sterile castes be separated from the alate line.

Thus fell away any factual evidence for a blastogenic theory of caste determination, leaving the field open once again and emphasizing the need for carefully controlled experimental studies.

Latest findings have emphasized the essential plasticity of the immature stages, as did the much earlier work of Grassi and Sandias and, more recently, that of Heath and Kalshoven. Kalshoven, like Heath, laid stress on the importance of the constitution of the group in determining the fate of individuals in it, and Castle (1934b) says of his own results, "Such vital modifications of individual development resulting from such slight changes in

colony composition illustrate the importance of individual interrelationships in maintaining the delicately balanced unity of a termite colony."

Even more recently, Miller (1942), in an excellent study of *Prorhinotermes simplex*, a primitive member of the family Rhinotermitidae, emphasizes the extreme plasticity of the nymphs. He finds that nymphs as late as the sixth instar are capable of becoming either soldiers or alates or of remaining as a doubtfully differentiated worker type.

My experiments with *Zootermopsis* have further emphasized this plasticity, indicating that it extends far beyond the sixth instar. Many of the large, broad-headed nymphs, termed soldier nymphs or, at times, soldiers by Heath (1927), are clearly of very late instar, some probably representing a tenth or even an eleventh stadium. These broad-headed nymphs are presumably capable of becoming ordinary apterous soldiers. Some of them, moreover, have wing rudiments, which may be lost or increased at subsequent molts. From such individuals, supposedly, arise some at least of the wing-padded soldiers occasionally encountered. The alate tendencies of these nymphs of advanced instar are in some instances, at least, carried to their ultimate conclusion and the nymphs become alates by a final molt (we have one authentic record). The alates with unusually large heads sometimes taken in flight may have this history. These alates would be in the tenth or eleventh instar, therefore, whereas Castle agrees with Heath that the alate stage is typically arrived at in the eighth instar. Another common history of these broad-headed nymphs is to become supplementary reproductives. Many broad-headed supplementaries are entirely apterous. Others have wing scars, or wing pads of varying size. Still others become the so-called fertile soldiers, or reproductive soldiers of Heath; actually, of course, these are supplementaries with more or less completely soldier-like heads.

It would seem most plausible to believe that the terminal types comprising alates, soldiers, workers where present, and individuals of precocious sexual maturity (neoténics) are end results of different developmental processes, each controlled by different genetic factors or patterns all of which are present in all individuals, and that the actual fate of each developing individual depends upon which of the several alternative genetic mechanisms comes into final play. Which of them does control the terminal developmental processes sup-

posedly depends upon certain as yet unknown differential factors in that part of the complex environment, social or otherwise, experienced by the particular individual. Since all colonies develop all castes, these factors must be considered to be present at some times or places in all colonies. These differential factors, or influences, have been variously suggested to be parasitic castration (Grassi and Sandias), differential feeding (Grassi and Sandias; Jucci, 1920, 1924; Heath; and others), differential relations to oxygen supply (Weyer, 1931), ectohormonal inhibitions (Pickens, 1932; Castle, 1934a, b; Light, Hartman, and O. H. Emerson, 1937), or, more vaguely, "the constitution of the colony" (Kalshoven, 1930).

It must be repeated that the nature of the mechanisms which cause the appearance of the different castes in every colony of every species of termites still eludes us. Neither published results of recent investigations nor findings of an extensive program of experiments carried out under my direction during the past eight years, unpublished as yet but drawn on for this review, give final solutions. (The work under my direction has been carried out by a corps of assistants under the immediate supervision of a number of research assistants of whom I wish especially to mention here Mr. Paul Illg, in charge for the last two years and now assisting me in organizing the data.) They serve rather to render obvious the complexities of the situation under investigation, to extend the area of investigation and indicate promising points of attack, and to emphasize the difficulties and pitfalls involved in laboratory studies of social animals, the lack of uniformity in experimental results, the consequent difficulties in obtaining satisfactory controls and the caution which must be exercised, therefore, in drawing conclusions from the data thus obtained.

Knowledge of conditions among the social Hymenoptera, especially the bees, is widespread among biologists, and confusion often arises from the assumption that conditions in the termites are largely comparable to those in the bees and ants. Both the Isoptera and the social Hymenoptera, it is true, exhibit polymorphism, and in each we find sterile castes. Here the resemblance ceases, however. In other features of their social organization the Isoptera differ radically from the social Hymenoptera. It has seemed necessary, therefore, in order to insure a clear understanding of the problems presented by the termite colony, to

accentuate here the most important features in which the social organization of the termites differs from that of the social Hymenoptera. This has been attempted in the twelve numbered statements which follow.

1. Sexual dimorphism is negligible in the termites.
2. The primary reproductives of termites are considered to constitute a single caste, consisting of equal numbers of males and females.
3. The male termite, so far as is known, is diploid (Stevens, 1905; Benkert, 1930; Light and McAuley, MS) and is almost certainly bisexually produced.
4. Parthenogenetically produced termites are exclusively females and therefore probably diploid as to chromosomes (thelytokous parthenogenesis; see Vandel, 1927, 1936).
5. There is nothing in the termites to correspond to the haploid parthenogenesis of the male Hymenoptera.
6. The method of sex determination is presumably simpler in the termites than in the Hymenoptera. At least, nothing is found in them comparable to the sex-intergrades and sex mosaics common among the Hymenoptera.
7. The termite colony is completely bisexual, all immature stages and all castes consisting of approximately equal numbers of males and females. There is no counterpart, therefore, of the exclusively female castes of the Hymenoptera and, consequently, in termites sex determination has nothing to do with caste determination.
8. The male is fully functional in the social life of the termite colony. Termite colonies are gynandrarchic, founded and headed by male and female, usually by a single pair, both sexes assisting in founding the colony and caring for the eggs and first brood.
9. The flight of termites, although followed by pairing, is not a mating flight, as in the social Hymenoptera generally, nor a swarming flight as in the bees. Copulation does not occur until some time after pairing.
10. The sterile castes of the termites are by no means homologous with those of the social Hymenoptera.

Especially it is to be noted that the terms soldier and worker used in connection with both ants and

termites have no significant common meaning for the two groups. Among termites the soldier caste is the older, nearly universal caste. The worker caste, on the other hand, is much more recent, being, in fact, a derivative of the soldier line (Emerson, 1926; Bathellier, 1927). The worker caste is altogether lacking in the large family of primitive termites, the Kalotermitidae, and has seemingly developed in the higher families since their separation from the lower families. Worker-soldier intergrades are practically unknown among termites, although neotenic soldier-nymphal intergrades occur commonly among lower termites.

11. The termites undergo long and gradual post-embryonic development involving numerous immature instars separated by molts, thus making possible permanent arrest of growth at various stages of development, or development in different stadia along different lines; all of which makes for complicated and plastic polymorphism.
12. In lower termites all of the work of the colony is done by nymphs of various instars, and even in the higher termites they take part in it, whereas the social Hymenoptera, being holometabolous, their immature stages add to but do not partake in the communal tasks.

THE NON-REPRODUCTIVE CASTES

All termites possess one or more non-reproductive or sterile castes, individuals of which develop in all colonies in fairly regular numbers. The sterile individuals are of two basically different types: (1) workers which are distinctly nymphal, apterous, eyeless individuals, and (2) soldiers which have highly altered, heavily sclerotized heads, and whose mandibles are either enormously enlarged or vestigial. Commonly a species possesses a single caste of soldiers and, among higher termites, a single type of workers. In some species of higher termites, however, there are two or even three castes of soldiers and also of workers. In some instances these different types of soldiers and workers are size segregants, terminal in different instars; in others they show distinct qualitative as well as quantitative differences (Hare, 1931). Workers are less universal in occurrence than soldiers. They are lacking as a caste in the large primitive family, the Kalotermitidae, and their status is doubtful in the other two lower families. Even in the Rhinotermitidae the status of the

worker caste seems doubtful (Pickens, Ph.D. thesis; Miller, 1942). As to their phylogenetic origin I am in full agreement with Emerson (1926) that they represent a fixation of individuals (nymphs) in the line of soldier development. In two species of higher termites soldiers have been shown to arise, supposedly by two molts, from nymphs which are of nearly the same size as workers and which differ from workers only slightly, in pigmentation, etc. (Emerson, 1926, *Constrictotermes*; Bathellier, 1927, *Nasutitermes*). Presumably, therefore, in the Nasutitermitinae at least, workers become adult in what is equivalent either to the penultimate or the antepenultimate instar of soldier development.

Two mechanisms seem necessary to produce a definite worker caste. One would operate at a definite stage in development to prevent further molting on the part of the individuals affected, thus making them terminal individuals—adults in that no further growth occurs. It may be presumed that this influence comes to bear in the stadium preceding the definitive worker stadium, probably, therefore, in the equivalent of the antepenultimate stadium in soldier development in species having a single worker type. Presumably, therefore, some apterous nymphs of this stadium become soldiers by two further molts and others become workers following a single molt. The second mechanism which must be invoked is one which controls the development of (1) special pigmentation (or in rare instances of color patterns), (2) of increased sclerotization, and (3), in higher termites, of certain structural details of the nota, the palpi and the antennae, characteristic of workers as contrasted to all other individuals of the colony.

I know of no evidence as to the factors operating to regulate the occurrence of workers in the termite colony. Until further evidence is available, it would seem best to suppose for reasons appearing in the discussion of soldier determination that the control of worker development is a negative one, those apterous nymphs of higher termites inhibited from soldier development becoming workers.

It is customary to say that there is no worker caste among the Kalotermitidae and this usage is best maintained if the word caste is to retain a definite meaning. It must be remembered, however, that nymphs of various types and instars do all the work in these colonies except in the earliest stages of colony inception, when the founding reproductives are the effective workers. In *Zooter-*

mopsis the nymphal stadia are numerous and long. Particularly important in these colonies are larger nymphs, typically apterous and therefore presumably in the soldier line. Many of these older apterous nymphs possess heads broader than those of the alate line and we have termed them broad-headed nymphs. Some of these must be in late instars, presumably the tenth or even the eleventh. It seems probable that we have here individuals which might well be considered to represent an incipient worker caste or at least to illustrate how such a caste may arise. Supposedly in the soldier line, they are in so late an instar that it seems unlikely they will or can molt into the soldier stage. That they are terminal cannot be proved, however, and indeed it is well known that they retain the ability to develop into supplementary reproductives. Further, they develop wing pads in some instances and one at least in our cultures actually completed development into an alate. Here again we have exemplified the plasticity characteristic, at least of the lower termites, but not, apparently, of the higher termites where intercastes are rare (see Adamson 1940).

All termites except those of the genus *Anoplotermes* possess a characteristic soldier caste. This all but universal occurrence of soldiers seems to indicate that the ancestral termite stock already possessed such a caste. In line with its ancient status and in contrast to the recent essentially nymphal worker caste, the soldier caste is marked by a strikingly distinct morphology, especially as regards head and mandibles. The morphological changes from nymph to soldier are very great and occur over a considerable period involving two stadia. In the stadium intervening between the last two molts in soldier development the nymph is correctly designated an ultimate soldier nymph or simply soldier nymph, although the already enlarged head and mandibles give it an unmistakable soldier-like appearance. Because of its difference from ordinary nymphs and its resemblance to the soldier, the ultimate soldier nymph has been termed a pseudo-nymph by Kalshoven and a pseudo-soldier by Castle. This instar has not been recognized by all students of termites and has been confused by some with recently molted unpigmented definitive soldiers under the name of callow soldiers, a term which should properly apply only to the recently molted definitive soldier. The ultimate soldier nymph stadium is short, the individuals remain incompletely pigmented and

are not able to take food, and the stadium serves essentially as does the pupal stage in holometabolous insects.

While the absence of soldiers in *Anoplotermes* has been generally considered to be secondary, it has been supposed that the loss was a permanent one involving degeneration or loss of the genetic mechanism. Goetsch (1939) has reported, however, that soldiers developed in incipient laboratory colonies founded by primary reproductives of a species identified by von Rosen as belonging to *Anoplotermes*. The nasute soldier obtained by Goetsch is not the type to be expected in *Anoplotermes* on the basis of the relationships indicated by the morphological features of the genus, especially those indicated by the structure of the nymphal mandibles (Emerson *in litt.*; see also Hare, 1937). Goetsch does not state on what von Rosen's identification was based, and it seems best to withhold acceptance of an *Anoplotermes* soldier, therefore, until examination of the workers produced in these colonies, or of the actual primary reproductives heading the colony, settles their taxonomic status. Mixed swarms are common in the tropics and the specimens sent von Rosen may have been different from those which founded the colonies.

All students of incipient colonies report the occurrence of usually one or at most a very few soldiers in each first brood. Castle's experiments and my own (see below) show unmistakably that the introduction of a soldier into an incipient colony usually prevents the appearance of the expected soldier. If the presence of soldiers in an incipient colony tends to prevent nymphs from completing development into the definitive soldier, then the presence of soldiers may be supposed to regulate by inhibition the occurrence of soldiers in older colonies. On this hypothesis soldiers would be expected to appear with regularity in groups of nymphs separated from older colonies, providing they do not include soldiers. Both Grassi and Kalshoven found that soldiers develop in groups of isolated nymphs. Kalshoven noted, however, as did Grassi, that soldiers thus produced seemed usually not to be perfect soldiers and suggested that they were neotenic.

Miller (1942) sought experimental evidence as to the influence of the presence of soldiers in regulating the number of soldiers in groups or colonies. His data do not lend themselves to summarization, but I shall attempt to sample the most significant of his results. Of 807 wing-padded individuals

set up in 21 groups without soldiers, 57 became soldiers, which was 18.5 per cent of the individuals which changed, whereas of 880 wing-padded individuals set up in 27 groups with soldiers, in a ratio of approximately 1 soldier to 3 wing-padded, only 6 became soldiers, or 2.5 per cent of the individuals which changed. In no group of the series with soldiers was more than one soldier produced, whereas of the 21 groups without soldiers 9 produced 2 or more soldiers (2 to 14). Miller (p. 26) concludes, with commendable caution, "The presence of adult soldiers in colonies of undifferentiated nymphs and of wing-padded forms had a slightly significant inhibiting influence on the development of additional soldiers."

In *Zootermopsis* I have found that soldiers very seldom occur in groups of nymphs isolated without soldiers, and at first sight this finding might seem to contradict the hypothesis that many nymphs tending to become soldiers are inhibited from further development in that direction by the presence of soldiers, or, conversely, that soldiers will shortly develop in groups lacking soldiers. Another explanation of these results seems more in line with facts, however. In groups of nymphs of *Zootermopsis* the tendency to neoteny is especially powerful, as will be seen later, and the individuals which most commonly become neotenic are just those nymphs, usually apterous, termed soldier-nymphs (or at times soldiers!) by Heath which could be expected to become soldiers. The onset of the shift toward precocious sexual maturity seems to arrest the individual in the instar in which it stands, or at most allows for but one molt (presumably when the individual is already near the molt). Thus perhaps, the neotenic drive supersedes in part at least the soldier drive, preventing soldier production in most groups. The so-called "nymphal soldiers" or "reproductive soldiers" which develop in some groups would seem to be well explained on this hypothesis being the result of the action of both drives in those individuals which were near the end of soldier development. As already noted, both Grassi and Kalshoven report deviation in the nymphal direction of soldiers produced under these conditions.

There seems to be no set proportion of soldiers in the colonies of *Zootermopsis nevadensis*. We have kept record for 74 colonies and find the percentage of soldiers to range from 0.49 to 12.49 per cent, with an average of 5.23 per cent. Grassi reported a ratio of 1 soldier to 5 nymphs in *Kaloterme flavi-*

collis. Miller found an even greater proportion of soldiers in *Prorhinotermes* ($1:3.6 \pm 0.55$ in stock colonies).

TABLE 2
Occurrence of soldier flares in natural colonies

SIZE OF COLONY	MONTH	PER CENT OF FIGMENTED SOLDIERS	PER CENT OF CALLOW SOLDIERS AND SOLDIER NYMPHS	TOTAL PER CENT SOLDIERS
4347	January	2.50	2.90	5.40
3650	January	7.64	3.42	11.06
2213	February	6.32	6.06	12.38
4830	February	2.05	9.40	11.45
1973	March	2.30	2.00	4.30
3629	March	2.75	3.72	6.47
3312	April	0.84	2.99	3.83
843	May	0.95	3.67	4.62
2414	May	1.70	0.82	2.52
4375	June	1.83	1.83	3.66
1616	June	4.82	4.33	9.15
7000	June	2.40	1.11	3.51
2535	July	6.82	4.42	11.24
2500	October	2.08	3.28	5.36
4200	October	1.32	1.93	3.25

There should be noted here certain indications that soldier development is cyclic in *Zootermopsis*. Certain colonies are found to have great numbers of ultimate soldier nymphs and callow soldiers, indicating flares of soldier production in colonies. Our records indicate that such flares occur at different times during the year (see Table 2). Alates,

although also seasonal in general, have been known to occur at almost all times of the year, and there is some evidence to indicate a correlation between these flares of soldier production and the presence of alates in the colony.

Neotenic nymphal-soldier intergrades, the so-called reproductive soldiers, have been mentioned. Intergrades between the soldier and alate castes do occur in termites. In one species, *Kaloterme occidentis* Walker, all soldiers are wing-padded and possessed of a compound eye larger than that common among the soldiers of primitive species. Wing-padded soldiers have been reported in other *Kalotermitidae*, but they are not the rule. In the *Rhinotermitidae* wing-padded soldiers have been reported for *Reticulitermes* by several authors (Grassi and Sandias; Pickens; Ghidini, 1938), and recently in *Prorhinotermes* by Miller. Such intercastes are evidently unusual among the higher termites, but Adamson (1940) reports them in *Microcerotermes arboreus* Emerson and *Nasutitermes guayanae* (Holmgren), and they may be expected to turn up in other species when these are carefully scrutinized.

A complication of the picture in *Zootermopsis* is the occurrence of wing-padded neotenic soldier-nymphal intergrades. Perhaps the soldiers of *Kaloterme occidentis* are not merely soldier-alate intercastes but supplementary reproductives. The rounded shape of the head in this species is suggestive of this but may be tied in with the alate influence.

(To be concluded)





CHEMISTRY OF "EYE COLOR HORMONES" OF *DROSOPHILA*

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INTRODUCTION

ALL biologists are familiar with the statement that hereditary factors or genes control the development of hereditary traits or characters. How, by what mechanism, they achieve this control is one of the great unsolved problems of physiological genetics. In recent years attempts have been made to approach the solution of this problem from different angles. One of these attempts, the study of the mechanisms of the genetic control of eye color differentiation in *Drosophila*, has made particularly rapid advances since 1935. Several reviews have been published on the progress in this field (Beadle, 1937; Ephrussi, 1938; Becker, 1938; Beadle and Tatum, 1941). The purpose of the present article is to review a particular line of this work, namely, that which has led to the knowledge of the chemical nature of some gene-controlled substances intervening in the development of eye colors in *Drosophila* and representing, so to say, the intermediate links between the genes controlling their production and the final character.

In presenting the results of the work along this line, the author has chosen to follow, as closely as possible, the chronological order. It is indeed probable that, in adopting this order, the author, who has to a certain extent contributed to the development of the subject, was guided by a sentimental impulse. Whatever the reason, the author feels that for him this is the easiest way to tell an "eye-witness" story, in which a series of "lucky accidents" played as important a rôle as the logic of the planned experiments. This alternation of logical steps and of the unforeseen will be in many ways suggestive to the unspecialized reader.

From the latter point of view it is, no doubt, worth noting that the relatively rapid advances of the work related in this article has been, in a great measure, due to a frank and wholehearted cooperation between the different workers, particularly

between the groups headed, at Stanford, by G. W. Beadle and, in Paris, by the present writer, and that, in this field of Biology, like in many others, the collaboration of biologists and chemists was a major factor in the achieved advances.

Vermilion in mosaics

The original facts which constitute the starting point of the work discussed in this review have been reported in 1920 by Sturtevant in a short paper published in the *Proceedings of the Society for Experimental Biology and Medicine*. In this paper Sturtevant has described the aberrant behavior of the mutant character vermillion in *Drosophila* gynandromorphs.

Gynandromorphs, that is, individuals composed of male and female parts, have been known in *Drosophila melanogaster* ever since this species has been extensively used in breeding experiments. Morgan and Bridges (1919) have made a detailed study of these exceptional individuals and have explained their origin through the elimination of one of the sex-chromosomes in the course of early cleavages. The study of sex-linked characters in these genetically mosaic individuals has shown that, as a general rule, "the male and female parts and their sex-linked characters are strictly self-determining, each part developing according to its own genetic constitution. No matter how large or small the region may be, it is not interfered with by influences coming from neighboring parts, nor is it overruled by the action of the gonads" (Morgan, Bridges and Sturtevant, 1925).

The aberrant case reported by Sturtevant in the above cited paper acknowledges the first exception to this general rule. A female heterozygous for the sex-linked genes eosin, ruby and forked was crossed with a male carrying in its X-chromosome the recessives scute, echinus, cut, garnet, vermillion and forked. Among the offspring of this cross a gynandromorph was found in which the male parts, including the head, showed the characters scute, echinus, cut, garnet and forked. The

female parts showed the forked character only. This appearance of the different parts of the fly was consistent with the interpretation that the animal started its development as a female carrying the maternal X-chromosome which was marked by the recessive genes listed above and that, in the course of one of the early cleavages, this chromosome was lost from one of the blastomeres, leaving the latter with the paternal X-chromosome only. However, on this interpretation, the eyes of the gynandromorph, whose head showed the paternal sex-linked characteristics, should show also the vermilion eye-color. This was not the case and from this observation Sturtevant has drawn the conclusion that "the non-vermilion color was then apparently determined not by the genetic constitution of the eye-pigment itself, but by some other portion of the body". Thus this short note contains the first description of a non-autonomous character in *Drosophila* and, in the quoted sentence, the first tacit assumption of the intervention of a diffusible substance in the process of eye color differentiation.

A similar behavior of vermilion was later observed by Bridges (1925) and L. V. Morgan (1929) in mosaics of different origin.

The importance of non-autonomous mendelian characters for the analysis of gene-controlled processes has been stressed by Sturtevant in his paper "The use of mosaics in the study of developmental effects of genes" read at the Sixth International Congress of Genetics (1932). In concluding this paper Sturtevant writes:

It is clear that in most cases there is a chain of reactions between the direct activity of a gene and the end-product that the geneticist deals with as a character. One may surmise that any valid generalizations about these reactions are more likely to concern the initial links than the terminal ones. However, it is the terminal ones that are usually more open to experimental attack, since the only index to the effectiveness of a given experimental technique is the condition of the end product. Looked at from this point of view, the type of experiment that I have described may be considered as a beginning in the analysis of certain chains of reactions into their individual links.

This paragraph is quoted *in extenso* because it contains, along with a clear and concise definition of the purpose of Sturtevant's experiments (and of later work derived from these experiments), a precise statement of the methodological limitations involved.

Transplantation in Drosophila

Although Sturtevant's interpretation of the behavior of vermilion in mosaics implied a humoral correlation, the direct demonstration of the existence of hormone-like substances in *Drosophila* was provided only in 1935, with the introduction of a transplantation technique adapted to this species (technique described by Ephrussi and Beadle, 1936). One of the first experiments performed with the help of the new technique was, so to say, a duplication of the situation which arose spontaneously in the case observed by Sturtevant. Eye discs of vermilion larvae were transplanted into wild type larvae and it was found that, under these conditions, the vermilion eye discs developed into adult structures showing the wild type color (Ephrussi and Beadle, 1935; Beadle and Ephrussi, 1936). Since the implanted eyes developed in the abdomens of the hosts without any constant or very definite connections with the surrounding tissues, it was concluded from these experiments that the lymph of the wild type hosts contained a substance responsible for the observed change from vermilion to wild type. Vermilion, the first non-autonomous character known in *Drosophila*, was therefore interpreted as a deficiency for a specific substance. This substance, produced under the control of the wild type allelomorph of the vermilion gene, represents then a link connecting this gene with the corresponding character (Fig. 1, A and B).

Essentially similar results have been obtained by a German group of workers with an eye-color mutant in the moth, *Ephesia kuhniella* (Caspari, 1933; Kühn, Caspari and Plagge, 1935). In the following pages, however, the main emphasis will be placed on the work with *Drosophila* because the existence in this species of a considerable number of eye color mutants has made possible a much further analysis.

The confirmation of the non-autonomous nature of vermilion led to the search for other non-autonomous eye colors. Over two dozen *Drosophila* eye-color mutants have been tested by transplantation experiments similar to those used with vermilion. Eye discs of the different mutant types have been transplanted into wild type hosts and their color characteristics were examined after hatching of the flies. Among the various eye colors thus tested, another eye color, cinnabar, characterized by a similar vermilion-like pigmentation, was found to be also non-autonomous.

Cinnabar eye discs transplanted into wild type hosts differentiated into eyes with wild type color. Following the reasoning applied in the case of vermilion, the conclusion was drawn that the wild type lymph contains a substance responsible for the change of pigmentation of implanted cinnabar eyes. And thus the question arose whether the change from cinnabar to wild type was caused by the same substance which controlled the change

from cinnabar to wild type. The wild type lymph contains both these substances. The lymph of the mutant cinnabar contains only one of them, namely the substance responsible for the change from vermilion to wild type. The mutant vermilion contains none of these substances. These two substances have been called respectively the v^+ and cn^+ substances or hormones, the exponent $+$ indicating their occurrence in the lymph of animals

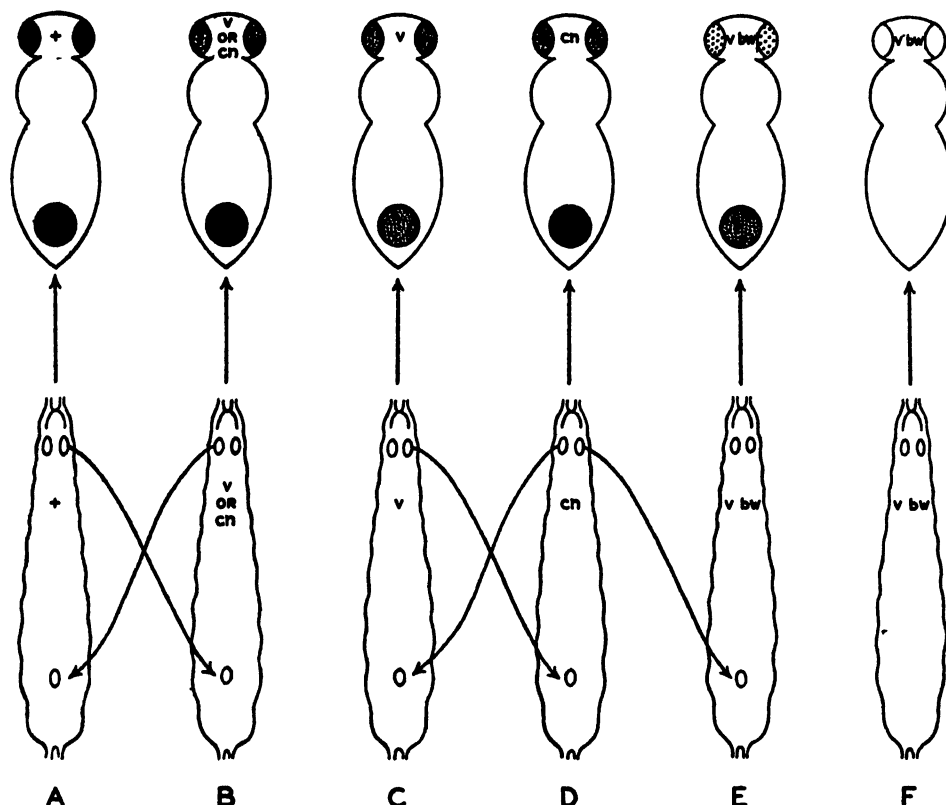


FIG. 1. SUMMARY OF THE RESULTS OF TRANSPLANTATION EXPERIMENTS

Below, host and donor larvae. Above, adult flies containing differentiated implants

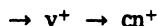
from vermilion to wild type or whether the wild type lymph contained two different substances. The answer to this question was given by other transplantation experiments (compare A, B, C, and D of Fig. 1) whose results are summarized in Table I and among which the two reciprocal transplantations (5 and 6) between cinnabar and vermilion are particularly significant.

The results of these reciprocal transplantations make it quite obvious that there are two different substances, one responsible for the change from vermilion to wild type and the other for the change

carrying the wild type allelomorphs of the genes vermilion (v) and cinnabar (cn) (Beadle and Ephrussi, 1936).

The above table contains only a few of the transplantations performed. In other transplantation experiments very numerous kinds of combinations have been realized between hosts and implants of different genetic constitutions. These experiments have lead to the important observation that, while a deficiency for the cn^+ substance alone characterizes the flies of certain genotypes, a deficiency or a decrease of concentration of the v^+ substance

is always accompanied by a deficiency or corresponding decrease of concentration of the cn^+ substance. On the basis of this observation the assumption was made by Beadle and Ephrussi (1936) that the two substances are formed in the course of a single chain of reactions, of which the v^+ substance represents the first and the cn^+ substance the second link:



This hypothesis, fundamental for the ensuing experimental developments, naturally did not imply a corresponding simplicity of the chain of reactions when translated in concrete chemical terms.

TABLE 1

Summary of results of transplantation experiments

IMPLANT	HOST	PHENOTYPE OF THE IMPLANT
1. Vermilion.....	Wild type	Wild type
2. Cinnabar.....	Wild type	Wild type
3. Wild type.....	Vermilion	Wild type
4. Wild type.....	Cinnabar	Wild type
5. Vermilion.....	Cinnabar	Wild type
6. Cinnabar	Vermilion	Cinnabar

In all transplantation experiments hitherto described, the observed changes in pigmentation were produced in the implants, under the influence of the new environment (host). However, effects of essentially the same sort can be produced as well in the opposite direction, i.e. changes can be induced in the pigmentation of the host eyes through an influence emanating from the implants. If, for example, a cinnabar eye disc is transplanted into a vermilion-brown larva (the reasons for choosing this type of double recessive host will be explained in a moment), the eyes of the host, normally containing but traces of pigment, show a marked darkening (Fig. 1, E and F). This result has been interpreted as a case of release of the v^+ substance produced by the implant.

This type of effect is mentioned here not because it is thought that it represents, in itself, something essentially new, but for the following two reasons. First, because effects of this type and, especially, reciprocal effects of the host on the implant and of the implant on the host, within the same experimental animal, further support the formation of the v^+ and cn^+ substances in the sequence indicated

above (see review by Beadle and Ephrussi, 1937); secondly and particularly, because of its technical value. The possibility of producing an effect on the eyes *in situ* has suggested a method for the detection of the diffusible substances in any material, for example in an extract. In other words, the finding of the effects on the hosts has supplied the basis for an assay technique indispensable in the early phases of all hormone work.

In the last mentioned experiment, double recessive vermilion-brown ($v\ bw$) flies were used instead of vermilion (v) flies, because in the almost colorless eyes of the double recessive a very slight change produced by the v^+ substance (i.e. a slight shift from the $v\ bw$ towards the v^+bw phenotype) is much more easily detected than in the eyes of vermilion flies. In other terms, the eyes of the vermilion-brown flies were found to constitute the most sensitive "detectors" of the v^+ substance. Similarly, cinnabar-brown flies can conveniently be used as "reagents" for the detection of the cn^+ substance.

The changes produced in the eyes of these detector flies by implants releasing one of the diffusible substances were found to vary according to the genotype of the implant (Ephrussi and Beadle, 1937). What is emphasized here is not the difference in the implants, but the variability of the effect. This variability was interpreted as indicating that the degree of darkening of the eyes was a measure of the amount of the diffusible substance released into the body fluid of the host. By selecting a series of flies of different genotypes, representing a series of intergrades between the phenotypes of vermilion-brown and brown flies, Tatum and Beadle (1938) have introduced a scale of standards which are comparable to various degrees of modification of the eye-color of vermilion-brown flies under the influence of the v^+ substance and can be evaluated in terms of arbitrary color values. The comparison of an experimental fly with this scale of standards permits the description of the results in terms of these color values, assumed to be related to the amount of v^+ substance by approximate proportionality. One of the first steps of the eye color modification, corresponding to one of the lighter shades in the scale of standards, was taken as indicative of the action of one arbitrary hormone unit. Thus the method of detection of the v^+ substance was transformed into a method of semi-quantitative determination of the hormone.

Transfusion of lymph

As shown above, the existence of the diffusible (v^+ and cn^+) substances has been postulated on the basis of, and offered as an interpretation for, the non-autonomous or dependent differentiation of the color characteristics of certain eye implants. A necessary corollary of this interpretation is that the postulated substances are transmitted from the locus of their production to the reacting organs (host or implanted eyes) through the lymph. The demonstration of their presence in the lymph should therefore be regarded as a supplementary proof of the correctness of the interpretation. This proof has been provided by direct lymph transfusion. The lymph of wild type or cinnabar pupae was injected into "detector" larvae. The flies which developed from the injected larvae showed a clear modification of the eye color, indicating that the injected lymph actually contained the postulated active substance (Beadle, Clancy and Ephrussi, 1937).

While this was a confirmation of the original hypothesis, there still remained one possible objection. The lymph contains, along with its liquid phase, cellular elements which may be held responsible for the modifications of the pigmentation. This objection was met by experiments in which the lymph, prior to injection, was frozen at very low temperatures and thawed several times and centrifuged in order to remove the residues of the destroyed cells. Lymph treated in this manner, when injected into vermilion-brown larvae, produced nevertheless clear modifications of the eye color and thus the experiments have shown that it is really the liquid phase of the lymph which carried the factors responsible for the changes in pigmentation (Harnly and Ephrussi, 1937).

The results just described were the first real indication that it should be possible to isolate the active principles. Before this could be attempted efficiently, however, several purely practical difficulties had to be solved. As in all chemical studies of hormones, the location of the source of active material to be extracted was thought to be particularly important in view of the exceptionally small size of the flies which constitute the natural source of the diffusible substances. Therefore the search was undertaken for another rich and easily available source of the hormones. Extracts of different tissues of higher animals were examined but all gave negative results. Yeast extracts were negative also. Lymph of different insects (*Galleria*

melonella, *Calliphora erythrocephala*, *Habrobracon juglandis*, *Ephestia kuehniella*, *Bombyx mori*, etc.) on the contrary, was found to contain substances which proved to be active in modifying the pigmentation in *Drosophila* (Ephrussi and Harnly, 1936; Beadle, Anderson and Maxwell, 1937). These experiments indicated then, in the first place, that the diffusible substances of *Drosophila* were not species-specific; secondly, they indicated a practical means for obtaining large quantities of extraction material.

Among the different insects rich in the v^+ and cn^+ substances, *Calliphora* was chosen, because the larvae and pupae of this species could be easily purchased in considerable amounts on the Paris market. Thus the first chemical characteristics of the diffusible substances were obtained from the study of extracts of *Calliphora* pupae.

Studies of extracts

That active extracts of the diffusible substances can actually be obtained was very soon shown by extracting *Calliphora* pupae in ethyl alcohol or ethyl alcohol-ether mixtures (Khouvine, Ephrussi and Harnly, 1936). The study of these extracts soon indicated that the active substances were soluble in water and in ethyl alcohol, insoluble in ether and chloroform. They were heat stable and dialysable. Therefore they were neither lipoids, enzymes, nor proteins (Khouvine and Ephrussi, 1937). These results were confirmed by Thimann and Beadle (1937) working with extracts of *Drosophila* pupae. Further study of both *Calliphora* and *Drosophila* extracts has shown that the diffusible substances are very unstable in acids and alkali and are not extractable in most organic solvents. They are precipitated by lead acetate and phosphotungstic acid as well as by Neubergs' reagent considered to be specific for amino-acids (Khouvine, Ephrussi and Chevais, 1938; Tatum and Beadle, 1938). Finally, the study of their rate of diffusion in agar blocks has indicated a molecular weight of 400-500 (Tatum and Beadle, *l.c.*). It should be pointed out here that throughout all these experiments the behavior of the v^+ and cn^+ substances and their properties appeared strictly identical and no separation of them has been possible.

Taken together, the results of all these studies have suggested the amino-acid like nature of the eye-color hormones and from this point on their further purification and eventual crystallization

was attempted. This line of work, however, has not led to the final identification of their chemical structure. While the results of the chemical work described above have played an important rôle in orienting the experiments which finally gave the clue, these experiments, as will be shown, were suggested by a different line of work.

Feeding experiments

In 1937 it was found that the diffusible substances will produce their effects on sensitive hosts not only when injected into the blood stream but also when administered *per os* (Beadle and Law, 1938). Since at that time it was already supposed, on the basis of the chemical investigations summarized above, that the active substances were amino-acids, it was realized that the "feeding technique" offered the possibility of testing various pure amino-acids or their mixtures for their hormone activity on a scale which was not accessible so long as it was necessary to resort to injections. Experiments were consequently started in which *Drosophila* (vermilion brown) larvae were raised on mixtures of agar, glucose and different amino-acids. It was assumed that these media would be sufficiently nutritive to support the completion of the growth and differentiation of larvae which, prior to the experiment (up to a certain rather advanced stage) were grown under standard food conditions. This assumption, however, appeared to be erroneous. In the first experiments only a low per cent of the larvae reached and went through metamorphosis. Only a few flies hatched, in a few of the experimental vials, and all these flies were of a very small size as a result of food insufficiency. However, the experiment led to an interesting observation. In one of the vials some flies developed a modified eye color, similar to that produced by a low dose of the v^+ substance. Was the amino-acid added to the medium in this vial responsible for the change? This was not certain since none of the control flies, raised on the agar glucose mixture without addition of amino acids, reached emergence. The repetition of the experiment on a large scale soon showed that this was not the case. In this new experiment eye color modifications were again observed, but they were observed in several vials containing very different amino acids. This pointed to the conclusion that the added amino acids were not involved at all in the observed effects. As a matter of fact, in this second experiment, some control

flies did hatch on a medium containing no added amino-acids, and these flies showed the eye color modification as well. Were then the observed effects due to some impurity in the agar or in the glucose? Control experiments were performed which showed conclusively that the eye color changes could not be ascribed to any one of the constituents of the medium and suggested that they were induced by the general malnutrition of the larvae (Khouvine, Ephrussi and Chevais, 1938). Special experiments performed in order to test this conclusion have shown that partial or total starvation of vermilion-brown larvae will produce the change from v towards v^+ , or, in other words, that under the influence of a certain diet, vermilion larvae, normally characterized by the inability to produce the v^+ substance, will be induced to produce it (Khouvine, Ephrussi and Chevais, *l.c.*; Beadle, Tatum and Clancy, 1938). This conclusion has been further confirmed by direct extraction of the v^+ substance from starved vermilion-brown larvae (Beadle, Tatum and Clancy, *l.c.*). Thus a very interesting relationship between the production of the v^+ substance and the general (probably protein) metabolism of the flies has been established. This relationship is an interesting problem of its own, but has no direct connection with the problem discussed here except for the practical conclusion concerning the feeding technique which had to be drawn from the results of these experiments. This conclusion pointed to the necessity of first working out an adequate nutritive medium into which the substances to be tested could be incorporated.

The effect of tryptophane

Among the different substances tested for their nutritive value, a peptone was tested and, while it appeared to be entirely satisfactory in so far as the general growth of the flies was concerned, its assay brought up a new and surprising result. Vermilion-brown flies raised on the medium containing the peptone also showed a modification of the eye-color, similar to that produced by starvation or by the addition of v^+ substance. In this case, however, the effect could hardly be attributed to a deficient diet and therefore seemed rather to indicate really the presence of an active principle in the peptone tested. Consequently experiments of the same type were repeated using several samples of peptones of different origins and various

proteoses. These experiments gave a very interesting result, namely that all the peptones tested, except one, gave positive results. The exceptional peptone was gelatin peptone which, as is well known, is characterized by the absence of tyrosin and tryptophane. The next obvious step then was the addition of tyrosin and tryptophane or their mixtures to the medium containing gelatine peptone. These experiments showed conclusively that tryptophane was the substance responsible for the eye color change.

But was tryptophane to be regarded as the v^+ substance? By definition, the v^+ hormone is a substance producing its characteristic effect when injected into the blood-stream. Tryptophane, however, when tested by injection, gave negative results. It became clear therefore that, while tryptophane could probably be regarded as a precursor of the v^+ substance, it could not be considered as being the substance itself. In other words, this finding made it quite probable that the v^+ hormone was a derivative of tryptophane. Consequently experiments were started in order to test the activity of various products of tryptophane transformation, both by feeding them to and injecting them into vermilion-brown larvae. This work has led to the finding of many tryptophane compounds active in the same way as tryptophane but inactive by injection (Khouvine and Ephrussi, unpublished). The work along this line has, however, been interrupted by the war and the decisive developments came from the combined results of two different lines of work, both starting from the discovery of the rôle of tryptophane in the described effects.

Bacterial synthesis of the v^+ substance

Throughout the experiments thus far described no particular attempt was made to control the growth of microorganisms in the media tested. In 1938 Tatum became interested in the nutritional requirements of *Drosophila* larvae and in connection with this work (Tatum, 1939b, 1941) established a technique for growing flies aseptically (technique described in Tatum and Beadle, 1939). One of the results of these studies of larval nutrition was the finding that media such as the agar-peptone mixtures used by Khouvine, Ephrussi and Chevais cannot support, under aseptic conditions, the normal growth and development of *Drosophila* larvae. The normal development of the flies in the experiments of these authors appeared there-

fore as probably due to the growth of microorganisms in these, by themselves deficient, media. If so, the hormone-like effects of starvation, peptones and tryptophane may have been due also to the intervention of microorganisms. With this idea in mind, Tatum and Beadle (1939) reinvestigated, under aseptic conditions, the effects of starvation peptones and tryptophane. While it was found that the starvation effect can be observed on flies grown under aseptic conditions, it appeared that the effect of tryptophane does not occur in the absence of microorganisms. The latter two effects were thus due to the presence of bacteria or yeast. In the course of these experiments, however, Tatum (1939a) found one vial accidentally contaminated by an aerobic bacillus. The vermilion-brown flies hatched in this vial showed a marked eye color modification. A culture of this unidentified *Bacillus* sp. was isolated from the contaminated vial and it was soon shown that the bacillus, when grown on a tryptophane-containing medium, synthesizes a substance similar in its effects and properties to the v^+ substance. The substance can be added to normal (complete) nutritive media and will produce the same effect. It therefore is clear that starvation plays no rôle in these results. Moreover, the substance extracted from the agar medium on which pure cultures of the bacillus were grown, was found to be active also when injected into vermilion-brown larvae. The method of extraction from the agar-medium showed that the solubilities of the active substance were similar to those ascribed to the v^+ substance on the basis of the chemical work related above. Finally, it should be mentioned that this substance produced effects only on vermilion-brown, not on cinnabar-brown flies. But Tatum (*l.c.*) was able to show that, like the v^+ substance, the substance obtained from bacterial synthesis, is converted, within the animal, to cn^+ substance. If vermilion-brown larvae, fed on a medium containing the substance synthesized by *Bacillus* sp. are, after pupation, boiled, crushed and fed to cinnabar-brown larvae, the latter develop into flies with a clearly modified eye color. Thus, the substance synthesized by Tatum's bacillus had all the known attributes of the v^+ hormone. Their identification required, however, their isolation in a pure state. The next step in the direction of this identification was made by Tatum and Beadle in 1940 when they succeeded in crystallizing the product of bacterial synthesis. On

the results of this work the authors report in the following terms:

... "This bacterially produced v^+ hormone has now been obtained in a pure crystalline state. The bacteria were grown on an agar medium containing dead yeast, sugar and l-tryptophane. The agar and yeast were precipitated in 80 per cent alcohol. The hormone was then taken up in a mixture of butyl alcohol, ethyl alcohol and water, and was finally precipitated from absolute butyl alcohol. It was then crystallized from 90 per cent ethyl alcohol. The crystals are very light yellow, elongated plates, usually forming in rosettes. The elementary analysis (made under the direction of Dr. A. J. Haagen Smit, of the California Institute of Technology) supports the empirical formula $C_{10}H_{10}N_2O_2$." (Tatum and Beadle, 1940).

It should be added that according to data of Tatum and Beadle one gram of this crystalline material will change from vermilion to wild type approximately one million flies.

The identification of the v^+ substance with kynurenine

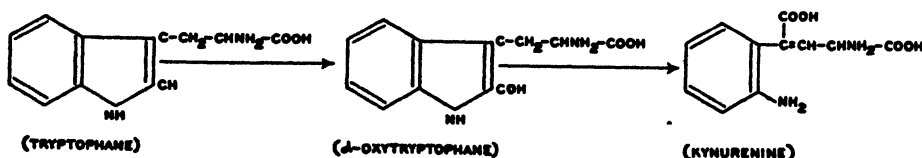
The knowledge of the structural formula of the v^+ substance, however, is connected with still another line of work and due to another group of workers. When the relation of the v^+ substance with tryptophane was established, tests of the activity of various tryptophane derivatives have been performed by Butenandt and his coworkers in Berlin. Among the substances tested, kynurenine, a substance discovered by Kotake in the urine of rabbits fed on l-tryptophane, gave positive results, both by the feeding and injection tests (Butenandt, Weidel and Becker, 1940a). Thus kynurenine was the first pure chemical of known

activity and isolated from bacterial synthesis is a sucrose ester of l-kynurenine.

The final proof of the identity of a chemically defined compound with the v^+ substance, however, should necessarily involve the demonstration of (1) the presence of the substance in flies which, according to transplantation experiments, contain it and (2) its absence in the mutant vermilion. Kikkawa (1941) has undertaken this work using the Otani-Honda method for the demonstration of kynurenine. The results of Kikkawa's work can be summarized as follows. Kynurenine can be detected in the mutant cinnabar and in its equivalent (mutant white-I) in *Bombyx*. From the eggs of the latter kynurenine sulphate has been obtained in crystalline form and shown to be active when injected into vermilion-brown *Drosophila* larvae. Tests for kynurenine in vermilion larvae and pupae are negative. Thus the first two criteria of the identification of kynurenine with the v^+ substance were fulfilled. However, the tests for kynurenine in wild type larvae and pupae were negative, while the original scheme of Beadle and Ephrussi calls for the presence of the v^+ substance in wild type lymph. Kikkawa assumes that these negative results are due to the rapid conversion of kynurenine into cn^+ substance (which is the compound responsible for the eye color change) and thus reconciles the scheme of Beadle and Ephrussi with the observed distribution of kynurenine.

The two remaining questions for which at least a partial answer can be given at present are those concerned with the origin and the fate of kynurenine.

According to Kotake, kynurenine is derived from tryptophane via α -oxy-tryptophane:



constitution whose physiological effects were found to be similar to those of the v^+ substance. The properties of kynurenine solutions are also similar to those of the highly active and highly purified solutions of the v^+ substance obtained from fly extracts. The results of Butenandt, Weidel and Becker made it very probable that kynurenine should be identified with the v^+ substance. This impression was further strengthened by the work of Tatum and Haagen Smit (1941) who were able to show that the crystalline product having v^+

This substance was only recently isolated by Wieland and Witkop (1940) from hydrolized phalloidin. Butenandt, Weidel and Becker (1940b) have injected solutions of α -oxy-tryptophane into vermilion-brown larvae and obtained positive, although weaker results than by injecting equivalent concentrations of kynurenine. It can be considered therefore that kynurenine arises from tryptophane via α -oxy-tryptophane *in vivo* also and α -oxy-tryptophane can be regarded as a precursor of kynurenine.

The nature of the cn^+ substance

Since the cn^+ substance is known to be derived from the v^+ substance and since the chemical nature of the latter seems to be established; it should be possible now to gain some insight into, if not determine the nature of, the cn^+ substance also. The most natural idea is to look for substances having a cn^+ activity among the derivatives of kynurenine.

stance, both found in human urine and responsible for Ehrlich's diazo-reaction, are derived from kynurenine. Although the solubilities of these substances are known to be different from those of the cn^+ substance, Kikkawa has applied the diazo-reaction to the mutants of *Drosophila* and *Bombyx* in which transplantation experiments have demonstrated the presence or the absence of the cn^+ substance. These tests have shown that

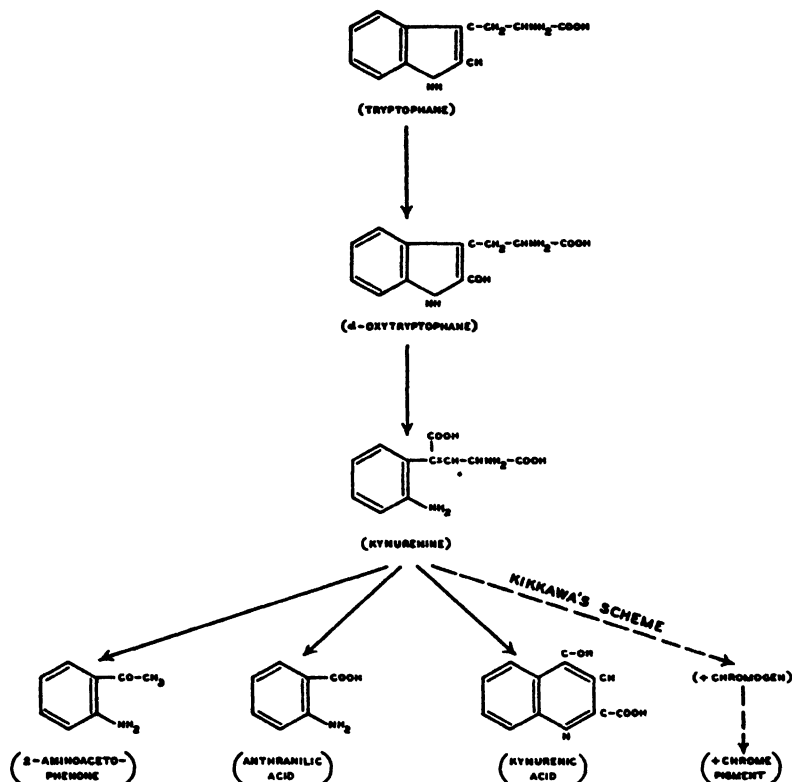


FIG. 2. THE PRODUCTS OF TRYPTOPHANE METABOLISM AND KIKKAWA'S SCHEME OF PIGMENT PRODUCTION IN *DROSOPHILA*

According to Kotake, in the animal body the transformations of kynurenine most commonly lead, through kynurenine-yellow, to *o*-amino-acetophenone, anthranilic acid and kynurenic acid (Fig. 2). The solubilities of the three first named substances suggest that they cannot be the cn^+ substance. Injections of anthranilic acid by Kikkawa (*l.c.*) in fact gave negative results. Kynurenic acid, as well as α -decarboxykynurenine have been tested by Butenandt, Weidel and Becker (1940b) and did not show any cn^+ activity.

Kotake has also suggested that the so-called Weiss urochromogen and the Sachs color sub-

stance, both found in human urine and responsible for Ehrlich's diazo-reaction, are derived from kynurenine. Although the solubilities of these substances are known to be different from those of the cn^+ substance, Kikkawa has applied the diazo-reaction to the mutants of *Drosophila* and *Bombyx* in which transplantation experiments have demonstrated the presence or the absence of the cn^+ substance. These tests have shown that

chromogen", thus indicating by the new term that the cn^+ substance is a direct precursor of the pigment.

PERSPECTIVES

The work of Kikkawa brings the story of the eye-color hormones of *Drosophila* up to date. Starting from the results of transplantation experi-

the future will be to connect these intermediate links with the two opposite ends of the chain.

The relation of kynurenine and of the cn^+ substance to the pigment is by no means clear, although Kikkawa, as mentioned above, assumes the cn^+ substance to be a precursor of pigment. Here, however, no major difficulty seems to stand in the way of future progress.

TABLE 2

Non-autonomous differentiation of vermillion in mosaics of *Drosophila melanogaster* (Sturtevant, 1920)

↓
Transplantation in *Drosophila* (Ephrussi and Beadle, 1935)

↓
Transfusion of lymph (Beadle, Clancy and Ephrussi, 1937)

↓
Non-species-specificity (Ephrussi and Harnly, 1936)

↓
Extraction of v^+ hormone (Khouvine, Ephrussi and Harnly, 1936)

↓
Purification and study of chemical properties of the v^+ hormone (Khouvine and Ephrussi, 1937; Thimann and Beadle, 1937; Tatum and Beadle, 1938)

Feeding technique (Beadle and Law, 1937)

↓
Effect of tryptophane (Khouvine, Ephrussi and Chevais, 1938)

↓
Bacterial synthesis of v^+ hormone (Tatum, 1939)

Crystallization of the v^+ hormone from bacterial synthesis (Tatum and Beadle, 1940)

Tryptophane metabolism in rabbits (Kotake, 1935)

↓
 v^+ activity of kynurenine (Bute-
mandt, Weidel and Becker, 1941)

Identification of v^+ hormone from bacterial synthesis with kynurenine (Tatum and Haagen Smit, 1941)

↓
Demonstration of kynurenine in *Drosophila* (Kikkawa, 1941)

ments which led to the postulation of the formation in sequence of two diffusible substances representing the first known links in the chain of reactions connecting the genotype with the character, we have now reached the point where a part of this chain can be described in chemical terms (Table 2 recapitulates the obtained results). The task of

Bridging the gap between the hormone-like substances which, at the present stage, are the first tangible manifestations of certain genes, with these genes, promises to be a much harder task. What is known at present of the action of the v^+ gene indeed suggests that this gene intervenes in the tryptophane metabolism by producing a spe-

cific oxidizing enzyme. Thus the problem of primary gene activity in this case seems to resolve itself into a problem of enzyme chemistry.

In so far as the primary genic action is concerned, however, we are confronted with more than purely practical difficulties. As Sturtevant (1941) puts it in discussing the methods of physiological genetics in a recent article:

"there is no *a priori* reason why the method may not, in certain cases, lead to a knowledge of the primary effect of a given gene; the difficulty is that, at present, there appears to be no way of deciding the point in any given case. That is to say, the chain of developmental reactions may be traced back to the gene, but there is

no way of determining when one has reached the gene" (p. 48).

The theoretical difficulty pointed out by Sturtevant is very real indeed. The present writer does not think, however, that the efforts along the same path should be abandoned. Instructed by the lessons of past experience and without underestimating the value of scientific planning, he keeps his optimism unaltered. It is his belief that unpredictable experimental situations often are the seeds of new insight and new ways of attack. Sometimes they do yield a little more than permitted by the theory.

LIST OF LITERATURE

- BEADLE, G. W. 1937. The development of eye colors in *Drosophila* as studied by transplantation. *Am. Nat.*, 71: 120-126.
- BEADLE, G. W., R. L. ANDERSON, and J. MAXWELL. 1938. A comparison of the diffusible substances concerned with eye color development in *Drosophila*, *Ephestia*, and *Habrobracon*. *Proc. Nat. Acad. Sci.*, 24: 80-85.
- BEADLE, G. W., C. W. CLANCY, and B. EPHRUSSI. 1937. Development of eye colours in *Drosophila*: Pupal transplants and the influence of body fluid on vermilion. *Proc. Roy. Soc. Lon.*, Ser. B., 122: 98-105.
- BEADLE, G. W., and B. EPHRUSSI. 1936. The differentiation of eye pigments in *Drosophila* as studied by transplantation. *Genetics*, 21: 225-247.
- BEADLE, G. W., and B. EPHRUSSI. 1937. Development of eye colors in *Drosophila*: Diffusible substances and their interrelations. *Genetics*, 22: 76-86.
- BEADLE, G. W., and L. W. LAW. 1938. Influence on eye-color of feeding diffusible substances to *Drosophila melanogaster*. *Proc. Soc. Exp. Biol. and Med.*, 37: 621-623.
- BEADLE, G. W., and E. L. TATUM. 1941. Experimental control of development and differentiation. Genetic control of developmental reactions. *Am. Nat.*, 75: 107-116.
- BEADLE, G. W., E. L. TATUM, and C. W. CLANCY. 1938. Food level in relation to rate of development and eye pigmentation in *Drosophila melanogaster*. *Biol. Bull.*, 75: 447-462.
- BECKER, E. 1938. Die Gen-Wirkstoff-Systeme der Augenausfärbung bei Insekten. *Naturwiss.*, 26: 433-441.
- BRIDGES, C. B. 1925. Elimination of chromosomes due to a mutant (Minute-N) in *Drosophila melanogaster*. *Proc. Nat. Acad. Sci.*, 11: 701-706.
- BUTENANDT, A., W. WEIDEL, and E. BECKER. 1940a. Kynurenin als Augenpigmentbildung auslösendes Agens bei Insekten. *Naturwiss.*, 28: 63-64.
- BUTENANDT, A., W. WEIDEL, and E. BECKER. 1940b. α -Oxytryptophan als "Prokynurenin" in der zur Augenpigmentbildung führenden Reaktionskette bei Insekten. *Naturwiss.*, 28: 447-448.
- CASPARI, E. 1933. Über die Wirkung eines pleiotropen Gens bei der Mehlmotte *Ephestia kühniella* Zeller. *Arch. Entw. Org.*, 130: 353-381.
- EPHRUSSI, B. 1938. Aspects of the physiology of gene action. *Am. Nat.*, 72: 5-23.
- EPHRUSSI, B., and G. W. BEADLE. 1935. La transplantation des disques imaginaux chez la *Drosophile*. *C. R. Acad. Sci. Paris*, 201: 98.
- EPHRUSSI, B., and G. W. BEADLE. 1936. A technique of transplantation for *Drosophila*. *Am. Nat.*, 70: 218-225.
- EPHRUSSI, B., and G. W. BEADLE. 1937. Development des couleurs des yeux chez la *Drosophile*: Influence des implants sur la couleur des yeux de l'hôte. *Bull. Biol.* 71: 75-90.
- EPHRUSSI, B., and M. H. HARNLY. 1936. Sur la présence chez différents insectes des substances intervenant dans la pigmentation des yeux de *Drosophila melanogaster*. *C. R. Acad. Sci. Paris*, 203: 1028-1029.
- HARNLY, M. H., and B. EPHRUSSI. 1937. Development of eye colors in *Drosophila*: Time of action of body fluid on cinnabar. *Genetics*, 22: 393-401.
- KHOUVINE, Y., and B. EPHRUSSI. 1937. Fractionnement des substances qui interviennent dans la pigmentation des yeux de *Drosophila melanogaster*. *C. R. Soc. Biol. Paris*, 124: 885-887.
- KHOUVINE, Y., B. EPHRUSSI, and S. CHEVAIS. 1938. Development of eye colors in *Drosophila*: Effect of yeast, peptones and starvation on their production. *Biol. Bull.*, 75: 425-445.

- KHOUVINE, Y., B. EPHRUSSI, and M. H. HARNLY. 1936. Extraction et solubilité des substances intervenant dans la pigmentation des yeux de *Drosophila melanogaster*. *C. R. Acad. Sci. Paris*, 203: 1542.
- KIKKAWA, H. 1941. Mechanism of pigment formation in *Bombyx* and *Drosophila*. *Genetics*, 26: 587-607.
- KÜHN, A., E. CASPARI, and E. PLAGGE. 1935. Über hormonale Genwirkungen bei *Ephestia kühniella*. *Z. Nach. Gesell. Wiss. zu Gott., Nach. a.d. Biol.*, 2: 1-30.
- MORGAN, L. V. 1929. Composites of *Drosophila melanogaster*. *Carn. Inst. Wash., Publ.* 399: 225-296.
- MORGAN, T. H., and C. B. BRIDGES. 1919. The origin of gynandromorphs. *Carn. Inst. Wash., Publ.* 278, 1-122.
- MORGAN, T. H., C. B. BRIDGES, and A. H. STURTEVANT. 1925. The genetics of *Drosophila*. *Bibliogr. Genetica*, 2: 1-262.
- STURTEVANT, A. H. 1920. The vermilion gene and gynandromorphism. *Proc. Soc. Exp. Biol. and Med.*, 17: 70-71.
- STURTEVANT, A. H. 1932. The use of mosaics in the study of the developmental effect of genes. *Proc. 6th. Int. Con. Gen.*, 1: 304-307.
- STURTEVANT, A. H. 1941. Physiological aspects of genetics. *Ann. Rev. Phys.*, 3: 41-56.
- TATUM, E. L. 1939a. Development of eye-colors in *Drosophila*: Bacterial synthesis of v^+ hormone. *Proc. Nat. Acad. Sci.*, 25: 486-490.
- TATUM, E. L. 1939b. Nutritional requirements of *Drosophila melanogaster*. *Proc. Nat. Acad. Sci.*, 25: 490-497.
- TATUM, E. L. 1941. Vitamin B requirements of *Drosophila melanogaster*. *Proc. Nat. Acad. Sci.*, 27: 193-197.
- TATUM, E. L., and G. W. BEADLE. 1938. Development of eye colors in *Drosophila*: Some properties of the hormones concerned. *Jour. Gen. Phys.*, 22: 239-253.
- TATUM, E. L., and G. W. BEADLE. 1939. Effect of diet on eye-color development in *Drosophila melanogaster*. *Biol. Bull.*, 77: 415-422.
- TATUM, E. L., and G. W. BEADLE. 1940. Crystalline *Drosophila* eye-color hormone. *Science*, 91: 458.
- TATUM, E. L., and A. J. HAAGEN SMIT. 1941. Identification of *Drosophila* v^+ hormone of bacterial origin. *Jour. Biol. Chem.*, 140: 575-580.
- THIMANN, K., and G. W. BEADLE. 1937. Development of eye colors in *Drosophila*: Extraction of the diffusible substances concerned. *Proc. Nat. Acad. Sci.*, 23: 143-146.





DEVELOPMENTAL PROCESSES AND ENERGETICS (Concluded)

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III. EVIDENCE OF ENERGY REQUIREMENTS

6. Respiration and rate of development of dwarf embryos

UNDER ordinary conditions the oxygen consumption may be taken as a measure of the energy turnover of the embryo. On this basis then two dwarf embryos should show a greater total oxygen consumption than one normal embryo when corresponding stages of development are attained. This increase could result from an increased rate of oxygen consumption while the rate of development remained the same, or it could result from a slower rate of development on the part of the dwarfs while the rate of oxygen consumption remained the same as in the normal embryos. The experiments show that the latter is the case.

The dwarfs in these experiments were produced by isolating the blastomeres in the two-cell stage of the sea-urchin egg. By suitable technique sufficient quantities of embryos could be obtained for the respiration measurements. As the data in Table 2 show, the rate of oxygen consumption (per mg. Kjeldahl nitrogen) of the dwarf embryos does not differ significantly from that of the normal embryos. This means that in the same time interval two dwarf embryos consume as much oxygen as one normal embryo. The dwarf embryos develop, however, at a much slower rate than the normal. They begin gastrulation at the normal time (at about 19 hours in *Echinus* at room temperature) but complete it and pass through later stages at a much slower rate than the controls. The delay in rate of development amounts to about 30 to 40 per cent. For example, in one experiment it took about five and a half hours for the dwarfs to complete gastrulation as compared with four hours in the controls.

Since oxygen consumption goes on at the normal rate in the dwarf embryos, and the rate of develop-

ment is slower, then, to reach the same stage of development, two dwarfs will consume more oxygen than one normal embryo. The increased oxygen consumption would amount to about 35 per cent if we take the beginning of gastrulation as a starting point. The expected value for the increased energy requirement (see above) is 41 per cent on the basis of a linear relation between force and wall thickness. Too much significance need not be attached to the actual figures at present.

TABLE 2
*Rate of oxygen consumption of dwarf embryos of the
sea-urchin*
(After Tyler, 1933.)

EXPERIMENT	AGE OF EMBRYOS IN HOURS	RATE OF OXYGEN CONSUMPTION IN CU. MM. O ₂ PER HOUR PER MG. KJELDAHL NITROGEN	
		Dwarf	Normal
A	15	21.2	20.7, 21.5
B	19	26.7	27.1, 25.6
C	19	26.7	25.5, 25.9
D	19	27.9, 27.1	27.8, 26.9
E	20	26.7	26.9, 27.8
F	22	27.0	27.9, 26.2
G	24½	28.1	29.3, 28.3

The important point is that the dwarf embryos do manifest the expected increase in total oxygen consumption. It seems quite reasonable too that this should be done by a retardation in rate of development rather than an increase in rate of oxygen consumption. There is no reason to expect the separation of the two cells in the two-cell stage to cause them to spontaneously increase their rate of oxygen consumption (i.e. above the normal rise that accompanies development), especially as we know that the rate of diffusion of oxygen is not a limiting factor in the sea-urchin egg at ordinary oxygen tensions (Amberson, 1928; Gerard, 1931; Tang, 1933).

The slower development of dwarf embryos has often been noted (see Tyler, 1933, for references). It has generally been attributed to a process called regulation which is assumed to require time. According to the present interpretation regulation (or whatever one might call the process which enables each of the two cells of the two-cell stage, when separated, to produce a normal embryo) does not require time. If such a re-adjustment process exists, it must, according to our view, be instantaneous. The slower development of the dwarf is regarded as being due to its having more than the normal amount of work to perform (per unit mass) while the energy supplying reactions (as measured by the oxygen consumption) go on at the normal rate.

Dwarf embryos of quarter-size (i.e. from isolated blastomeres of the four-cell stage) develop more slowly than do dwarfs of half-size. This is to be expected on the basis of the present analysis, although one could invoke regulation (a greater time needed for the quarter-size dwarfs) to account for it. Another interesting case is that of the dwarfs of unequal size produced by Spemann and Falkenberg (1919) in the salamander. They found that the smaller of the pair of twins developed more slowly than the larger partner, and, rather than to invoke regulation, they suggested that the retardation might be connected with the smaller size.

On the other hand, Horstadius and Wolsky (1936) have found it necessary to use the concept of regulation time in some highly interesting work on bilateral symmetry in the sea-urchin egg. They present evidence for the existence of a bilateral organization of the egg in the early cleavage stages. In pairs of dwarf embryos that presumably come from separating the dorsal and ventral sides of the egg it is found that the dorso-ventral axis is inverted in the dorsal partner while it is unchanged in the ventral partner. Both develop into normal plutei. The dorsal partner, however, is observed to develop at a slower rate than the ventral dwarf, both developing slower than the whole embryo. The greater retardation on the part of the dorsal dwarf is interpreted as due to time being required for regulation. This difference is not exhibited by "right" and "left" partners, both being about equally retarded in comparison with the whole embryo. Horstadius and Wolsky are of the opinion that both factors, regulation time as well as the energy relations, may be involved in the retardation exhibited by the dwarf embryos, the two views not being mutually exclusive.

Horstadius and Wolsky also found that dwarf embryos of one-eighth the normal size could develop to the pluteus stage. Previous investigators have never been able to get embryos from isolated blastomeres of the eight-cell stage to go beyond gastrulation. As a possible explanation for this failure it was suggested (Tyler, 1935) that the available energy is used up in the early stages in performing the relatively increased work of differentiation in one-eighth-sized embryos. This was evidently an overstatement since it is now shown that the $\frac{1}{8}$ embryos can reach the pluteus stage. The necessary feature, according to Horstadius and Wolsky, is that the original fragments be composed of both animal and vegetal material of the egg, and this is accomplished by operating at the 32-cell stage instead of the eight-cell stage. It would, however, be of interest to know whether there are differences in diameter and thickness of wall in the beginning gastrula stage between the embryos obtained by these two methods. The finding that $\frac{1}{8}$ embryos can develop to the pluteus stage does not by any means conflict with our view, since all that we are justified in expecting is that they should develop more slowly than the $\frac{1}{4}$ embryos, if they bear the same dimensional relation to the whole embryo.

7. Giant embryos

The viewpoint that we have developed is further supported by the behavior of giant embryos. Driesch (1900) first showed that normal embryos of giant size could be obtained by the fusion of two fertilized eggs. On the assumption that time is required for regulation then the giant embryos should develop more slowly than the controls, since there must be at least as much regulation involved in the production of a single embryo from two eggs as in the production of two embryos from a single egg. On the other hand the expectation from the present analysis is that the giant embryos should develop more rapidly than the controls. Experiments undertaken to test this (Tyler, 1935) showed that the latter is the case.

The experiments were performed on eggs of three different species of sea-urchin. The eggs were fused in the one-, two-, or four-cell stage. Most of the fused eggs develop into double monsters of various sorts. Normal giant embryos were obtained from the fused eggs in fourteen cases. Ten of these developed faster than the controls and four developed at the same rate as the controls. None developed slower. The acceleration can be ob-

served in the gastrula stage as Fig. 2 illustrates. In later stages the difference in rate becomes more marked. Thus, in the case showing the biggest difference in rates, the giant completed gastrulation at 26 hours after fertilization as compared with 30 hours for the control, and entered the pluteus stage at 45 hours as compared with 64 hours for the control. The average for all the cases observed

produced giant and dwarf embryos by cutting two beginning gastrulae of *Triton* parasagittally, one to the left, the other to the right of the mid-line, and fused the two larger pieces together as well as the two smaller pieces. In the cases in which both fused embryos developed normally, the giant embryo developed markedly faster than the dwarf embryo.

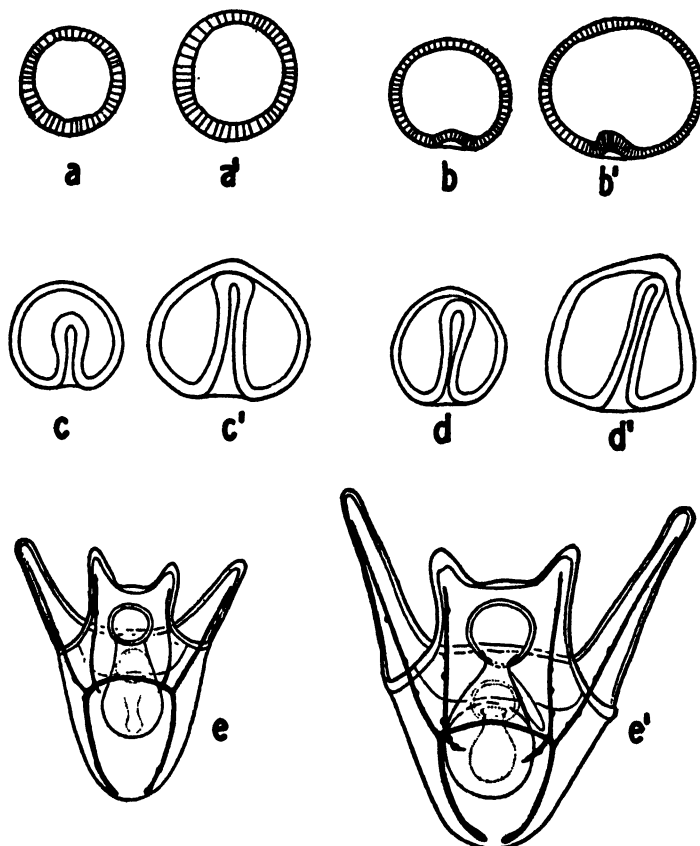


FIG. 2. NORMAL (a to e) AND GIANT (a' to e') SEA-URCHIN EMBRYOS OF IDENTICAL AGES

The more rapid development of the giants is manifest in the late gastrula and prism stages (c, c' and d, d'). The plutei (e and e') were drawn at 3½ days, but the giant entered this stage at 64 hours and the normal at 82 hours. (After Tyler, 1935.)

(including the four showing no increase) amounted to 1.4 times the control rate if the beginning of gastrulation is taken as the starting point. The number of cases is, of course, not sufficiently large to attach much quantitative significance to this value. The main point is that the giant embryos do develop more rapidly than the controls.

This more rapid development on the part of giant embryos was noted by Spemann and Bautzmann (1927) in some experiments on salamander eggs performed with other purposes in view. They

Another instance that may be cited is the faster development of giant limbs which Filatow (1932) observed. By grafting a limb-bud of one salamander embryo on to that of another embryo in the same stage a normal giant limb could be produced and it was found to differentiate more rapidly than the control limb on the unoperated side. This result, too, fits in with the view that there is relatively less work of differentiation in relation to the energy supplied in the case of the giant structure.

Filatow also produced giant eyes by fusing presumptive optic cup material. But in this instance no acceleration was observed; neither was there a retardation. The difference may be that the optic cup develops within the embryo and so the enlarged structure may encounter greater resistance on the part of the adjacent, normal-sized structures, whereas the limb grows out from the embryo and is relatively free of such resistance.

8. Thick-walled embryos

In the dwarf embryos from isolated blastomeres the wall thickness, in the blastula and gastrula stages, is the same as in the normal. It is therefore proportionately too thick. In the giant embryo the wall thickness is again the same as in the normal embryo, hence relatively too thin. For further investigation of this factor of relatively increased wall thickness it would be desirable to have thick-walled embryos of normal size. It was found in echinoderms (Tyler, 1937) that embryos having in the blastula and gastrula stages thicker than normal walls, could be produced by relatively simple treatment of the eggs.

These embryos develop from what are called "tight membrane eggs", which are simply eggs in which the fertilization membrane fails to separate off from the surface but remains closely adjacent to the egg. Tight membrane eggs are produced by short treatment with acid sea water or isosmotic non-electrolyte solutions. They sometimes occur spontaneously. The tight membrane eggs develop into normal plutei, but the early stages are considerably modified. The presence of the tight membrane around the egg opposes the increase in diameter that normally takes place as the blastocoel forms. Thus at the time of hatching the blastocoel is considerably smaller and the wall correspondingly thicker than normal. The difference is maintained through the gastrula stage, although both tight membrane embryos and normal embryos are continuously increasing in diameter and decreasing in wall thickness.

At gastrulation, then, the tight membrane embryo (Fig. 3b') has a thicker wall than the control (Fig. 3b), but it is also smaller in diameter. It does not, therefore, quite meet the requirements we have set. We can, nevertheless, state our expectations as to its rate of development. Proceeding as before a normal embryo is compared with a hypothetical embryo of the same diameter as the tight membrane embryo but with a proportion-

ately normal wall thickness. Then this hypothetical embryo is compared with the actual "tight membrane" embryo. Without going through the details it may be stated that for similar form changes (gastrulation, etc.) the "tight membrane" embryo should require more energy than the normal. If the rate of energy supply is the same in

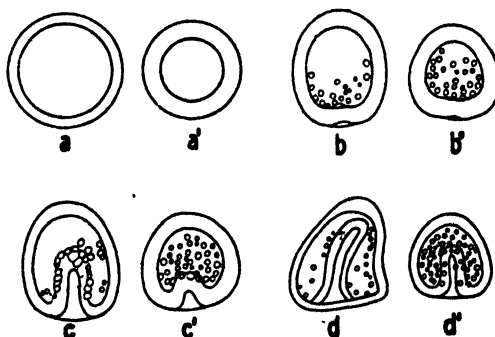


FIG. 3. NORMAL (a to d) AND THICK-WALLED (a' to d') SAND DOLLAR EMBRYOS OF IDENTICAL AGES

The typical retardation in rate of development of the thick-walled embryos is shown in the gastrula and prism stages (c, c' and d, d'). (After Tyler, 1937.)

TABLE 3

Retardation of "tight membrane" embryos of *Dendraster*
(After Tyler, 1937.)

STAGE OF DEVELOPMENT	AVERAGE TIME OF DEVELOP- MENT AT 20°C.		INCREASE IN TIME FROM THE BEGINNING OF GASTRU- LATION
	Normal	Tight mem- brane	
		hours	hours
Beginning gastrula	12	12	0
$\frac{1}{2}$ gastrulated	14	16	100
$\frac{2}{3}$ gastrulated	15	19	133
Early prism	16	22	150
Late prism	21	26 $\frac{1}{2}$	61
Early pluteus	23 $\frac{1}{2}$	31	65
Late pluteus	52	68	40

both then the "tight membrane" embryo should develop slower than the normal

This is in fact found to be the case. The tight membrane eggs show the same rate of respiration as the controls while they develop at a much slower rate. The retardation in development is illustrated in Fig. 3. Gastrulation begins at the same time in both but is completed much sooner in the normal embryo. The retardation is proportionately greater in the gastrula and early prism stages than in the later stages, as Table 3 shows. It

differs in this respect from the results with dwarf embryos where the retardation remains proportionately the same in all stages. This difference is probably due to the fact that the tight membrane egg finally attains, in the pluteus stage, the normal dimensions. There are other complicating factors in the "tight membrane" embryos such as the abnormal distribution of the mesenchyme cells which may have an effect on the rate of development. Until the effect of such factors are assessed it is not profitable to attempt to push the analysis much further. All we can say at present is that the finding that development is retarded in these embryos while the rate of respiration is unaltered agrees with the expectation on the basis of the dimensional reasoning.

TABLE 4

Temperature coefficients for cleavage and later stages of development of sand-dollar (Dendraster) eggs

(After Tyler, 1936a.)

	15.0°/ 25.0°	12.0°/ 22.0°	8.0°/ 18.0°	15.0°/ 20.0°	10.0°/ 15.0°
2-cell stage.....	2.21	2.82	3.88	1.62	2.01
4-, 8-, and 16-cell stages.....	2.24	2.80	3.82	1.60	1.96
Gastrulation.....	2.20	2.79	3.98	1.60	1.99
Prism.....	2.17	2.79	3.86	1.63	2.04
Pluteus.....		2.84	3.94	1.65	2.03

The figures give the averages of the ratio of the time to reach a particular stage at the lower temperature to the time at the higher temperature.

IV. EFFECT OF TEMPERATURE ON RATE OF CLEAVAGE AND RATE OF DIFFERENTIATION

Change in temperature will, as is well known, alter the rate of development. It is conceivable, then, that the processes of differentiation, growth and maintenance might be differently affected by change in temperature. But in experiments on the eggs of several marine animals (Tyler, 1936) no evidence was found of a differential effect. We assume as before that cleavage is an index of growth in the type of egg under consideration. The results show that change in temperature affects the rate of attainment of the various stages of differentiation to the same extent as it affects the rate of cleavage. This is illustrated in Table 4 for the eggs of the sand-dollar. The range of temperatures employed practically covers that in which development is normal. Similar results were ob-

tained with the eggs of sea-urchins (*Strongylocentrotus* and *Lylechinus*), ascidians (*Ciona*) and worms (*Urechis*).

The results were checked in another way; namely, by determining the number of cells present in embryos reared at two different temperatures when identical stages of differentiation are attained. If cell division and differentiation are differently affected by temperature there should be differences in cell number in embryos raised at different temperatures. The determinations of cell number show no significant differences. We may conclude, then, that growth and differentiation cannot be dissociated by means of temperature, at least within the normal range.

Experiments employing supramaximal temperatures have been performed on frog embryos by Hoadley (1938) who also reviews earlier work on the subject. Among a number of interesting effects Hoadley notes a suppression of gastrulation while cell division continues (as evidenced by the resulting small cells) as a result of transferring early blastulae to the higher temperature. Another effect noted is a retarded utilization of yolk in some of the high temperature embryos. There is, then, as Hoadley points out, evidence that the various developmental processes may be dissociated by this means. Recently Ryan (1941b) has presented evidence that in the frog some dissociation can be effected by temperature within the normal range. He finds that the temperature coefficients for stages of embryo formation differ from those for cleavage stages, although the coefficients are constant within the various cleavage stages, as well as within the various later stages.

V. EFFECT OF TEMPERATURE ON RATE OF RESPIRATION AND RATE OF DEVELOPMENT

It is of interest to know whether the rate of respiration (which we assume measures the rate of energy supply) varies in the same way with change in temperature as does the rate of development. In the earlier work the results are conflicting. More recent experiments (Tyler, 1936; Atlas, 1938) show that the temperature coefficients for rate of respiration and rate of oxygen consumption are the same. This is illustrated in Table 5, which gives some of the data obtained with eggs of the sea-urchin. Identity of the temperature coefficients means that during the same developmental period at different temperatures there will be the same total oxygen consumption, and that is what the

figures in Table 5 show. Similar results are obtained with sand-dollar, worm, ascidian and frog eggs.

Regardless, then, of the temperature (within the normal range) an embryo will consume the same amount of oxygen in reaching a given stage of development. There is no optimum temperature at which development is accomplished with a minimum respiration.

The results may be interpreted to mean that change in temperature does not alter the proportions in which the available energy is utilized by maintenance, growth and differentiation, or that there are compensatory changes in the requirements for these processes. The latter seems unlikely but the possibility cannot be readily dismissed.

eggs do not differ significantly over most of the temperature range in which development occurs. At the lower temperature intervals there may in some cases be significant differences, but there are not sufficient data to determine this point. In the different species investigated the change in rate of respiration upon fertilization varies considerably, but this apparently bears no relation to the values of the temperature coefficients.

Bodine (1932) determined the temperature coefficients of the rate of oxygen consumption of diapause (resting) and developing grasshopper embryos. The rate of respiration is greatly reduced in the diapause stage as compared with the pre- or post-diapause stages, but the temperature coefficients are found to be the same.

The similarity of the temperature coefficients of

TABLE 5

Oxygen consumed by eggs and embryos of the sea-urchin (Strongylocentrotus) during the same developmental period at different temperatures
(After Tyler, 1936b.)

TIME AFTER FERTILIZATION AT START OF MEASUREMENTS	TEMPERATURES		RESPIRATION TIME		CU. MM. O ₂ PER MG. EGG NITROGEN	
	Higher	Lower	Higher temp.	Lower temp.	Higher temp.	Lower temp.
	°C	°C	hours	hours		
45 minutes.....	20	15	1.0	1.36	6.7, 6.8	6.2, 6.6
35 minutes.....	20	10	1.0	2.3	6.4, 6.3	6.5, 6.1
50 minutes.....	20	7.5	1.0	3.2	6.4, 6.3	6.2, 6.3
18½ hours.....	20	15	3.0	4.11	65, 67	68, 69
21½ hours.....	20	15	3.0	4.11	72, 75	75, 77

The rate of respiration of unfertilized eggs is also known to vary with temperature. Since an unfertilized egg may be considered a resting cell it should exhibit simply maintenance (basal) metabolism. This does not mean that its respiratory rate should be lower than that of the fertilized egg. In fact Whitaker (1933) has shown that in some species the rate is higher before than after fertilization. We might, however, expect the temperature coefficients of the respiratory rate to be the same in unfertilized as in fertilized eggs. This was investigated in some experiments on marine eggs by Rubenstein and Gerard (1934) and by Tyler and Humason (1937). While there are differences in the results of the two sets of investigations that need yet to be resolved, we shall use the data of the latter investigators as a basis for discussion. Table 6 summarizes most of the data. The temperature coefficients of the resting and of the developing

TABLE 6

Temperature coefficients (average Q₁₀'s) for rate of oxygen consumption of resting and of developing eggs
(After Tyler and Humason, 1937.)

	TEMPERATURES	RESTING EGGS	DEVELOPING EGGS
<i>Strongylocentrotus</i>	22° and 12°C	2.54	2.4
	20° and 10°C	2.6	2.3
	18° and 8°C	2.6	2.6
	17.5° and 7.5°C	2.7	2.8
<i>Urechis</i>	22° and 12°C	2.6	2.7
	20° and 10°C	2.5	2.9
<i>Ciona</i>	25° and 15°C	1.9	2.2
	22° and 12°C	2.0	2.5
<i>Dendraster</i>	22° and 12°C	2.6	2.8

the respiratory rate in unfertilized and in fertilized eggs does not quite answer the question as to the possibility of compensating effects which was mentioned above. In adult physiology the maintenance (basal) metabolism is measured by the respiration or the heat production under "resting" conditions. It is tacitly assumed that the measurements give the amount of energy actually required under the particular conditions; that is, that there is an exact adjustment between requirement and production. It is difficult to regard the situation in any other way. An adjustment of this kind seems to be illustrated in muscle physiology by the "Fenn effect" (Hill, 1931). Fenn (1924) showed that if a muscle is allowed to shorten and do work the total energy at its disposal is greater than when it contracts isometrically, i.e. without doing work. But to determine whether this sort of thing occurs in the case of maintenance we would want to know what the maintenance requirements are or at least how they would vary with changing conditions (temperature, etc.).

We have regarded maintenance as the processes opposing the death of the cell. The unfertilized egg, as we know, dies within a limited time after being shed. A study of the life span and respiration of unfertilized eggs under various conditions might then be expected to yield further information concerning these processes. Recent work on this subject (Whitaker, 1937; Schechter, 1937; Tyler, Ricci and Horowitz, 1938) shows that the life span may be prolonged in various ways without necessarily altering the respiration. But this work does not as yet add very much to our knowledge of maintenance.

VI. THE RISE IN RESPIRATORY RATE DURING DEVELOPMENT

We have regarded the developmental changes as dependent on the respiration, the rate of oxygen consumption being taken as a measure of the energy available for the various processes. We may consider now the possibility that the developmental changes determine in turn the rate of respiration.

It has been known, since the measurements of Warburg (1908) on sea-urchin eggs, that the rate of respiration rises during development. The increase in rate is not directly proportional to the increase in number of cells (cf. Needham, 1931). It might, nevertheless, depend upon changes brought about by cell division. To examine this question we would want to block or retard cleavage

by some agent that does not alter the initial respiration. That is, we must exclude a direct effect of the agent employed on the rate of respiration. Then if the rise is subsequently affected it may be related to the failure of the cleavage processes. These conditions have been met in some recent experiments by Brachet (1938) and Tyler and Horowitz (1938).

Brachet found that if eggs of the annelid, *Chaetopterus*, are activated with KCl the initial respiration is the same as that of the fertilized eggs but the increase in rate occurs much more slowly. The eggs activated with KCl undergo what has been called "differentiation without cleavage" (Lillie, 1902). Actually, mitotic processes do occur in these eggs. Pasteels (1934) and Brachet (1937) have shown that the eggs after extruding polar bodies undergo a series of monaster cycles during which there is an increase in number of chromosomes and lobulations simulating cleavage. But the furrows disappear. The various changes and the attainment of the ciliated trochophore-like stage proceeds much more slowly than in the case of the fertilized egg. Also thymonucleic acid synthesis, which may be taken as a chemical index of mitotic activity, is greatly retarded in the treated eggs. The retarded rise in rate of respiration roughly parallels the retardation in the developmental changes.

Tyler and Horowitz obtained quite similar results with eggs of the gephyrean worm; *Urechis*. The non-cleaving eggs were produced in this case by means of a short treatment with dilute ammonia. Here again the initial respiration is the same as that of the fertilized eggs but the rise is greatly retarded (see Figs. 4, A, A', B, B'). In addition measurements were also made on cleaving eggs produced by means of a somewhat longer treatment with ammonia. In this case the rise in respiratory rate (Figs. 4, C, C') is more rapid than with the non-cleaving eggs, but it is still considerably slower than with the fertilized eggs. Cleavage in these eggs is correspondingly slower than in the fertilized eggs. Measurements were also made on fertilized eggs in which cleavage is inhibited by means of phenylurethane (Figs. 4, D). With the proper concentration of phenylurethane cytoplasmic division may be inhibited without any immediate effect on the respiratory rate. Nuclear division continues but at a retarded rate. Again the rise in respiratory rate is retarded.

If it were possible to block completely the mitotic

activity without altering the initial respiration one would expect complete failure of the rise to occur. But that is a rather ideal situation which is evidently not easily attained. The present results, however, furnish strong evidence that changes brought about in the egg by its developmental activity determine the rate of respiration. On the assumption that mitosis is an index of growth in this type of egg we might regard the rise in respiration as a function of growth.

Earlier than the above-mentioned experiments Lindahl (1936, 1938) has shown that Lithium in-

substrate during the period of combustion of another. In sea-urchin eggs he (1940b) has further examined the respiratory rise by artificially producing *Dauerblastulae* through the action of thiocyanate. The respiratory rate of the *Dauerblastulae* does not rise above the level characteristic of the normal blastula. Here again the initial respiration is unaffected by the treatment and the failure of the rate to rise above the blastula level is evidently the result of the inhibition of development that occurs at that stage in the thiocyanate-treated eggs.

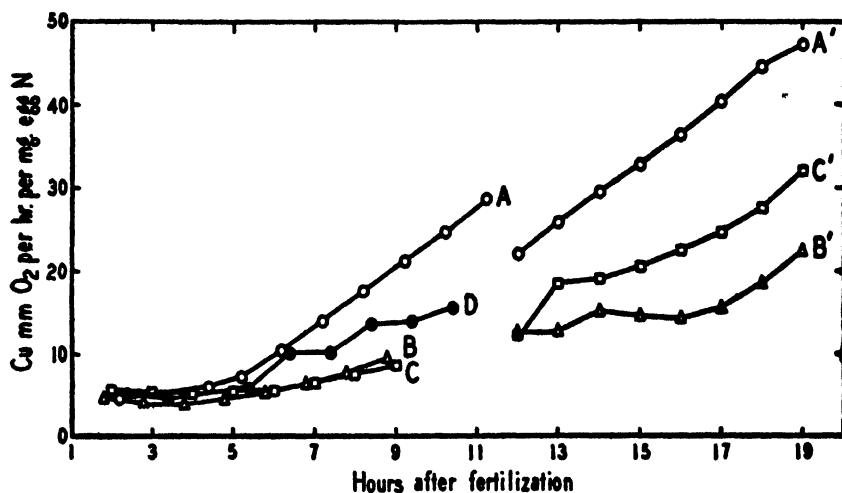


FIG. 4. RATE OF OXYGEN CONSUMPTION OF URECHIS EGGS AT 22°C.

Curves A and A', normal fertilized eggs; B and B', non-cleaving artificially activated eggs; C and C', cleaving artificially activated eggs; D, phenylurethane-treated eggs. A', B' and C' are not direct continuations of A, B and C since the eggs had been cultured at a lower temperature (18°C) for 11 hours previous to the measurements. (After Tyler and Horowitz, 1938.)

hibits the rise in rate of respiration of the sea-urchin egg while the initial rate is unaffected. This is of particular interest because of the rather specific morphological effects of Lithium (exogastrulation, etc.) and Lindahl attempts to relate the retardation of the rise to the "endodermalising" effect produced. It may be noted, however, that Lithium has a decided retarding influence on development, as MacArthur (1924) and others have shown. But no information is given by Lindahl as to the rate of cleavage, etc. of the treated eggs.

A careful study has been made recently by Horowitz (1940a) of the rise in respiratory rate and the respiratory quotient of developing eggs of *Urechis*. His findings extend to this type of egg Needham's view of a succession of energy sources in ontogeny, resulting from factors operating within the developing tissues and not alterable by the addition of one

VII. OXYGEN DEBT

One of the reasons for considering the rate of oxygen consumption as an index of the energy supplied is that development stops under anaerobic conditions. There is, however, evidence that the cessation of development does not occur immediately upon the attainment of complete absence of oxygen (cf. Needham, 1931). This limited development under anaerobic conditions would be a serious objection to the view that oxygen consumption is a measure of the energy supply, unless it can be shown that the egg builds up a debt for oxygen equivalent to the amount of development it undergoes.

This question has been investigated by Brachet (1934) on eggs of the frog, and he finds convincing evidence of the existence of an oxygen debt. Developing eggs that have been subjected to anaero-

biosis show upon return to air a much higher rate of oxygen consumption than the controls. After a short time the rate drops to the control value, indicating that the debt has been paid off. Brachet also notes that with identical periods of anaerobiosis the intensity of the debt does not increase in the course of development, although as we know the rate of respiration rises. This is of interest in connection with the fact that greater developmental progress is made when eggs are subjected to anaerobiosis in earlier stages than in later stages of development. While Brachet has not shown that the total oxygen consumed to reach a given stage in development is unaltered by the introduction of a period of anaerobiosis, his results make that extremely likely.

Whether the debt corresponds to the oxidation of metabolites accumulated during anaerobiosis or to the reconstitution of an oxidising reserve was examined by determining the respiratory quotient after anaerobiosis. In the latter case (which is essentially an oxygenation without CO_2 production) the R.Q. should be abnormally low, and that is what is actually found.

VIII. CAN DEVELOPMENT BE ACCELERATED?

A question that often occurs to embryologists is whether it is possible to speed up the rate of development above that at the highest temperatures that an egg will stand. It is, of course, well known that the time of metamorphosis of amphibian tadpoles can be advanced by the administration of thyroxin and other agents. But we do not regard this as an acceleration of development. The work of Rowntree (1936, 1937) and his collaborators on the effect of injecting thymus extract in rats through succeeding generations are perhaps more to the point. But the results do not appear to be as yet generally accepted.

An acceleration of development following inhibition has been reported recently by Buchanan (1938, 1940) in salamander embryos. If the embryos are subjected to a low temperature (6°C) for short periods (up to 6 days), it is found that on subsequent development at the control temperature (21°C) they practically overtake the controls by the time that stage is reached at which the balancers are lost. Acceleration is noted in earlier stages too. Buchanan's methods have been criticized by Ryan (1941a) who in turn, however, presents statistical evidence that the rate of cleavage and of later development in *Rana pipiens* is accel-

ated by an exposure to low temperature. He also reports an acclimatization after the increase in rate so that eventually the rate becomes that which is normal for the higher temperature.

Aside from these cases that have been mentioned there does not appear to be any evidence that development can be accelerated. There are several agents such as certain oxidation-reduction dyes (Barron, 1929; Runnström, 1930) and the substituted phenols (Clowes and Krahle, 1936, 1938) that are known to increase greatly the rate of respiration of developing eggs. But these agents rather than tending to accelerate development, either have no effect or inhibit it. There are a number of possible reasons why the acceleration of respiration should not necessarily result in a speeding up of development, even if we grant that the energy for development comes ultimately from the respiration. The stimulation by these agents might involve a short circuiting of the energy supplying mechanism. Or there may be concomitant injurious effects on the eggs. This seems to be particularly the case with the oxidation reduction dyes that have been employed, the concentrations giving a stimulation of respiration having a toxic action on the eggs. With the substituted phenols, however, no injurious effect is produced.

Another possibility appears in the results of Runnström's interesting experiments with respiratory stimulants. Runnström (1935) shows that pyocyanine stimulates only part of the respiration of the fertilized sea-urchin egg. The part of the respiration stimulated by pyocyanine is not inhibited by HCN and appears thus to be similar to the respiration of the unfertilized egg. Also, according to Lindahl and Öhman (1938) the amount of stimulation with pyocyanine decreases as the respiration rises (i.e. as development proceeds). It would seem then that this type of agent acts on a part of the respiration not directly concerned with the developmental changes.

The exact reason for the failure of these agents to work may very well be different in each case. It would, nevertheless, be of interest to determine the reason in order to learn what kind of treatment might be expected to accelerate development as well as to learn something of the nature of embryonic respiration. Possibly a substance less foreign to the egg should be employed. It has in fact been reported that echinochrome, which is obtained from the eggs, the blood and the test of sea-urchins, gives a 16-fold rise in the respiratory rate of the

unfertilized sea-urchin egg (Friedheim, 1933). This is far greater than has been obtained with any other agent ever employed. However, attempts (Tyler, 1939) to repeat these results have been unsuccessful.

While a stimulation of respiration need not result in a speeding up of development, a lowering by inhibiting agents should give a corresponding retardation in developmental rate provided that any oxygen debt that may be incurred is taken into account. There are a number of agents that are known to inhibit the respiration in a more or less reversible manner (e.g. cyanide, carbon monoxide, etc.). They also retard development. But whether the effect on development corresponds exactly to the effect on the respiration has never been determined. One reason is evidently that development cannot be slowed up very much with the chemical agents so far employed without injurious effects. More suitable agents are apparently required.

Considerable progress has been made in recent years in the elucidation of the mechanism of cellular respiration and fermentation. Ferments, active groups and protein carriers have been isolated as pure substances by Warburg and his collaborators, Theorell, Euler and others (see reviews by Warburg, 1937; Michaelis and Smythe, 1938; Northrop and Herriott, 1938). With these substances respiration and fermentation systems can be set up *in vitro* in which carbohydrate is broken down in quite specific ways. The cell structure is unessential for the reactions to proceed, since they go on in aqueous solution. But it is evidently essential for the transfer of energy and the coordination of the metabolic processes. Runnström (1937) has recently reviewed the relatively little work that has been done on the relation between cell structure and metabolism. While there are no general conclusions yet to be drawn, it is from investigations in this field that we may hope to learn something of the mechanism of energy transfer and utilization. This would be of importance not only in determining how development may be accelerated, but in further analysis of the factors responsible for the developmental changes.

IX. SUMMARY

An attempt has been made in this review to define the various fundamental processes that are involved in development, and to evaluate the evidence concerning their dissociability as a preliminary to a discussion of the energy requirements of

differentiation in particular. The evidence obtained from observations on developing embryos under naturally occurring, as well as experimentally produced, conditions is shown to afford justification for distinguishing between the processes of maintenance, growth and differentiation (and its components) in development. At the same time the close integration of these processes in normal development and the conditions under which they are inter-dependent are manifest in many of the experiments discussed.

A theoretical discussion is presented of the energy requirements in development and more especially for the processes of differentiation since it is that which characterizes the developing embryo. This is considered from the point of view of the chemical changes (synthesis) and mechanical changes (alterations of shape) that may be involved. The type of information needed and the difficulties involved in a direct demonstration and evaluation of the requirements are shown to point toward the desirability of an indirect method of attack. This is supplied by the application of the principle of similitude (dimensional analysis) to the results of experiments with dwarf embryos. The general applicability of this principle to other problems of biodynamics is indicated. In the case of embryonic differentiation the work shows the existence of a distinct energy requirement for the process, and the conclusion is shown to be substantiated in experiments with giant embryos and thick-walled embryos.

The action of temperature on rate of development and rate of respiration is discussed from the point of view of the developmental processes and energy requirement vs. production. It is shown that there is no optimum temperature at which development is accomplished with a minimum of respiration.

The normal rise in respiratory rate that occurs during development is shown to be dependent upon changes brought about by cell division. The existence of the ability, on the part of developing eggs, to build up a debt for oxygen is demonstrated and objections to the view that oxygen consumption is a measure of the energy supply are thereby removed. The possibility of accelerating development is examined particularly in relation to respiratory stimulants.

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LIST OF LITERATURE

- ALLEN, B. M. 1916. The results of extirpation of the anterior lobe of the hypophysis and of the thyroid of *Rana pipiens* larvae. *Science*, 44: 755-757.
- . 1938. The endocrine control of amphibian metamorphosis. *Biol. Rev.*, 13: 1-19.
- AMBERSON, W. R. 1928. The influence of oxygen tension upon the respiration of unicellular organisms. *Biol. Bull.*, 55: 79-91.
- ARON, H. 1910. Wachstum und Ernährung. *Biochem. Zeit.*, 30: 207-226.
- . 1911. Nutrition and growth. *Philip. Jour. of Sci.*, B 6: 1-50.
- ASTBURY, W. T. 1933. Fundamentals of Fibre Structure. Oxford Univ. Press.
- ATLAS, M. 1938. The rate of oxygen consumption of frogs during embryonic development and growth. *Physiol. Zool.*, 11: 278-291.
- BARRON, E. S. G. 1929. III. The effect of methylene blue on the oxygen consumption of the eggs of the sea-urchin and starfish. The mechanism of the action of methylene blue on living cells. *Jour. Biol. Chem.*, 81: 445-457.
- BAUTZMANN, H. 1929. Über bedeutungsfremde Selbstdifferenzierung aus Teilstücken des Amphibienkeimes. *Naturwiss.*, 17: 818-827.
- BERRILL, N. J., and HUSKINS, C. L. 1936. The "resting" nucleus. *Amer. Nat.*, 70: 257-260.
- BLOOM, W. 1937. Cellular differentiation and tissue culture. *Physiol. Rev.*, 17: 589-617.
- BODINE, J. H. 1932. Hibernation and diapause in certain Orthoptera. II. Response to temperature during hibernation and diapause. *Physiol. Zool.*, 5: 538-548.
- BOHR, C., and HASSELBALCH, K. A. 1903. Ueber die Wärmeproduktion und den Stoffwechsel des Embryos. *Skandin. Arch. Physiol.*, 14: 398-429.
- BORSOOK, H. 1935. Reversible and reversed enzymatic reactions. *Ergeb. Enzymforsch.*, 4: 1-41.
- BRACHET, J. 1934. Étude du métabolisme de l'oeuf de Grenouille (*Rana fusca*) au cours du développement. *Arch. de Biologie*, 45: 611-727.
- . 1937. La différenciation sans clivage dans l'oeuf de *Chétophtère* envisagé aux points de vue cytologique et métabolique. *Arch. de Biologie*, 48: 561-589.
- . 1938. The oxygen consumption of artificially activated and fertilized *Chaetopterus* eggs. *Biol. Bull.*, 74: 93-98.
- BRADLEY, H. C. 1938. Autolysis and atrophy. *Physiol. Rev.*, 18: 173-196.
- BRIDGEMAN, P. W. 1931. Dimensional Analysis. Yale Univ. Press, New Haven.
- BUCHANAN, J. W. 1938. Developmental acceleration following inhibition. *Jour. Exp. Zool.*, 79: 109-128.
- . 1940. Developmental rate and alternating temperatures. *Jour. Exp. Zool.*, 83: 235-248.
- BYERLY, T. C. 1926. Studies in growth. I. Suffocation effects in the chick embryo. *Anat. Rec.*, 32: 249-270.
- CARREL, A. 1938. See Parker, 1938.
- CASTLE, W. E., and GREGORY, P. W. 1929. The Embryological basis of size inheritance in the rabbit. *Jour. Morph.*, 48: 81-104.
- CLARK, F. N. 1938. Grunion in Southern California. *Calif. Fish and Game*, 24: 49-54.
- CLOWES, G. H. A., and KRAHL, M. E. 1934. Action of dinitro compounds on sea-urchin eggs. *Science*, 80: 384-385.
- , and —. 1936. Studies on cell metabolism and cell division. I. On the relation between molecular structures, chemical properties, and biological activities of the nitrophenols. *Jour. Gen. Physiol.*, 20: 145-171.
- COLE, K. S. 1932. Surface forces of the *Arbacia* egg. *J. Cell and Comp. Physiol.*, 1: 1-9.
- DARESTE, C. 1882. Recherches sur la production des monstres, dans l'oeuf de la poule, par l'effet de l'incubation tardive. *Compt. Rend. Acad. Sci.*, 95: 254-256.
- . 1891. Recherches sur la Production Artificielle des Monstrosités. C. Reinwald & Cie., Paris.
- DAWSON, A. B. 1937. Persistence of cytoplasmic differentiation during mitosis. *Amer. Nat.*, 71: 605-609.
- Dictionary of Applied Physics. 1922. Ed. by R. Glazebrook. Vol. I, p. 82.
- DRIESCH, H. 1891. Entwicklungsmechanische Studien. I. Der Werth der beiden ersten Furchungszellen in der Echinodermentwicklung. Experimentelle Erzeugung von Theil- und Doppelbildung. *Zeit. Wiss. Zool.*, 53: 160-184.
- . 1900. Studien über Regulationsvermögen der organismen. 4. Die Verschmelzung der individualität bei Echinidenkeimen. *Arch. Entw.-mech.*, 10: 411-434.
- DÜRKEN, B. 1926. Das Verhalten embryonaler Zellen im Interplantat mit Berücksichtigung des Geschwulstproblems. *Arch. Entw.-mech.*, 107: 727-828.
- . 1935. Über Bestrahlung des Organisatorbezirks im Tritonkeim mit Ultraviolett. *Zeit. wiss. Zool.*, 147: 295-356.
- ELLIS, E. 1933. The influence of sulfhydryl groups and respiration on the rate of cell division. *Jour. Cell. and Comp. Physiol.*, 4: 127-139.
- FENN, W. O. 1924. The relation between the work performed and the energy liberated in muscular contraction. *Jour. Physiol.*, 58: 373-395.
- FILATOW, D. 1932. Entwicklungsbeschleunigung in Abhängigkeit von einer künstlichen vergrößerung der Anlage. Versuche an Amphibienaugen und extremitäten. *Zool. Jahrb.*, 51: 589-634.

- FISCHER, A., and PARKER, R. C. 1929. Dauerzuchtung in vitro ohne Wachstumsbeschleunigung. *Arch. exp. Zellforsch.* 8: 325-339.
- FRIEDHEIM, E. A. H. 1932. Sur deux ferments respiratoires accessoires d'origine animale. *Arch. Sci. Phys. et Nat. (Geneva)*, 14 (suppl.): 179-182.
- GERARD, R. W. 1931. Oxygen diffusion into cells. *Biol. Bull.*, 60: 245-268.
- GREGORY, P. W., and CASTLE, W. E. 1931. Further studies on the embryological basis of size inheritance in the rabbit. *Jour. Exp. Zool.* 59: 199-212.
- GRODZINSKI, Z. 1934. Über die Entwicklung von unterkühlten Hühnereiern. *Arch. Entw.-mech.*, 129: 502-521.
- GUDERNATSCH, F. 1912. Feeding experiments on tadpoles. I. The influence of specific organs given as food on growth and differentiation. *Arch. Entw.-mech.*, 35: 457-483.
- , and HOFFMAN, O. 1937. A study of the physiological value of α -amino acids during the early periods of growth and differentiation. *Arch. Entw.-mech.*, 135: 136-177.
- HAHN, H. 1936. Autolyse. *Ergeb. Enzymforsch.*, 5: 117-158.
- HAMLETT, G. W. D. 1933. Polyembryony in the armadillo: Genetic or physiological? *QUART. REV. BIOL.*, 8: 348-358.
- HAMMETT, F. S. 1940. Chemical structure and its relation to growth and development. *Am. Jour. Roentgen. and Rad. Ther.*, 43: 266-270.
- , and REIMANN, S. P. 1940. Chemical specificity in growth and development. *Ann. Int. Med.*, 13: 1483-1488.
- HARVEY, E. N. 1931. A determination of the tension at the surface of eggs of the annelid *Chaetopterus*. *Biol. Bull.*, 60: 67-71.
- HEILBRUNN, L. V. 1937. An Outline of General Physiology. Saunders, Philadelphia.
- HERBST, C. 1893. Experimentelle Untersuchung über den Einfluss der veränderten chemischen Zusammensetzung des umgebenden Mediums auf die Entwicklung der Thiere. *Mitth. Zool. Stas. Neapel*, 11: 136-220.
- HILL, A. V. 1931. Adventures in Biophysics. Univ. of Pennsylvania Press, Philadelphia.
- HOADLEY, L. 1929. Differentiation versus cleavage in chorio-allantoic grafts. *Arch. Entw.-mech.*, 116: 278-299.
- , 1930. Some effects of $HgCl_2$ on fertilized and unfertilized eggs of *Arbacia punctulata*. *Biol. Bull.*, 58: 123-144.
- , 1938. The effect of supramaximum temperatures on the development of *Rana pipiens*. *Growth*, 2: 25-48.
- HOLTFRETER, J. 1929. Über die Aufzucht isolierter Teile des Amphibienkeimes. I. Methode einer Gewebezüchtung in vivo. *Arch. Entw.-mech.*, 117: 421-510.
- , 1931. *Ibid.* II. Züchtung von Keimen und Keimenteilen in Salzlösung. *Arch. Entw.-mech.*, 124: 404-466.
- , 1933a. Nachweis der Induktionsfähigkeit abgetöteter Keimteile. Isolations- und transplantationsversuche. *Arch. Entw.-mech.*, 128: 584-633.
- , 1933b. Die totale Exogastrulation, eine Selbstablösung des Ektoderms vom Entomesoderm. Entwicklung und funktionelles Verhalten nervenloser Organe. *Arch. Entw.-mech.*, 129: 669-793.
- , 1938. Veränderungen der Reaktionsweise im alternden isolierten Gastrulaektoderm. *Arch. Entw.-mech.*, 138: 163-196.
- HOROWITZ, N. H. 1940a. The respiratory metabolism of the developing eggs of *Urechis caupo*. *Jour. Cell. & Comp. Physiol.*, 15: 299-308.
- , 1940b. Comparison of the oxygen consumption of normal embryos and Dauerblastulae of the sea-urchin. *Jour. Cell. & Comp. Physiol.*, 15: 309-316.
- HÖRSTADIUS, S. 1928. Über die Determination des Keimes bei Echinodermen. *Acta Zool.* 9: 1-192.
- , and WOLSKY, A. 1936. Studien über die Determination der Bilateralsymmetrie des jungen Seeigelkeimes. *Arch. Entw.-mech.*, 135: 69-113.
- HOUWINK, R. 1934. Physikalische Eigenschaften und Feinbau von Natur und Kunstharzen. *Leipzig*.
- , 1937. Elasticity, Plasticity and Structure of Matter. Cambridge University Press.
- HUFFMAN, H., ELLIS, E., and FOX, S. 1936. Thermal data. VI. The heats of combustion and free energies of seven organic compounds containing nitrogen. *Jour. Amer. Chem. Soc.*, 58: 1728-1733.
- HUXLEY, J. 1932. Problems of Relative Growth. *London*.
- JACKSON, C. M. 1936. Recovery in rats upon re-feeding after prolonged suppression of growth by dietary deficiency of protein. *Amer. Jour. Anat.*, 58: 179-193.
- , 1937. Recovery of rats upon re-feeding after prolonged suppression of growth by under-feeding. *Anat. Rec.*, 68: 371-381.
- , and STEWART, C. A. 1920. The effects of inanition in the young upon the ultimate size of the body and of the various organs in the albino rat. *Jour. Exp. Zool.*, 30: 97-128.
- KELVIN, LORD and TAIT, P. G. 1903. Treatise of Natural Philosophy. Cambridge University Press.
- KRAHL, M. E., and CLOWES, G. H. A. 1938. Physiological effects of nitro- and halo-substituted phenols in relation to extracellular and intra-

- cellular hydrogen ion concentration. *Jour. Cell. & Comp. Physiol.*, 11: 1-40.
- KUSCHE, W. 1929. Interplantation umschriebener Zellbezirke aus der Blastula und Gastrula der Amphibien. I. Versuche an Urodelen. *Arch. Entw.-mech.*, 120: 192-271.
- LANGMUIR, I. 1938. The speed of the deer fly. *Science*, 87: 233-234.
- LEHMANN, F. E. 1937a. Die Wirkungsweise chemischer Faktoren in der Embryonalentwicklung der Tiere. *Rev. Suisse de Zool.*, 44: 1-20.
- . 1937b. Mesodermisierung des präsumptiven Chordamaterial durch einwirkung von Lithiumchlorid auf die Gastrula von *Triton alpestris*. *Arch. Entw.-mech.*, 136: 112-146.
- LENNERSTRAND, A. 1933. Aerobe und anaerobe Glykolyse bei der Entwicklung des Froscheies (*Rana temporaria* L.). *Zeit. vergl. Physiol.*, 20: 287-290.
- LEPESCHKIN, W. W. 1937. Zell-Nekrobiose und Protoplasma-Tod. Protoplasma Monographien 12. Borntraeger, Berlin.
- LEWIS, W. H. 1903. Experimental studies on the development of the eye in amphibia. *Amer. Jour. Anat.*, 3: 1-3.
- . 1904. Experimental studies on the development of the eye in amphibia. I. On the origin of the lens. *Rana palustris*. *Amer. Jour. Anat.*, 3: 505-536.
- LILLIE, F. R. 1902. Differentiation without cleavage in the egg of the annelid *Chaetopterus pergameneus*. *Arch. Entw.-mech.*, 14: 477-499.
- . 1906. Observations and experiments concerning the elementary phenomena of embryonic development in *Chaetopterus*. *Jour. Exp. Zool.*, 3: 153-268.
- LINDAHL, P. E. 1936. Zur Kenntnis der physiologischen Grundlagen der Determination im Seeigelkeim. *Acta. Zool.*, 17: 179-365.
- , and ÖHMAN, L. O. 1938. Weitere Studien über Stoffwechsel und Determination im Seeigelkeim. *Biol. Zentralbl.*, 58: 179-218.
- LOEB, L. 1901. On the transplantation of tumors. *Jour. Med. Research*, 6: 28-40.
- . 1926. Transplantation and potential immortality of mammalian tissues. *Jour. Gen. Physiol.*, 8: 417-440.
- LOVE, A. E. H. 1927. A Treatise on the Mathematical Theory of Elasticity. 4th ed. Cambridge University Press.
- MACARTHUR, J. W. 1924. An experimental study and a physiological interpretation of exogastrulation and related modifications in echinoderm embryos. *Biol. Bull.*, 46: 60-87.
- MEYERHOFF, O. 1911. Untersuchungen über die Wärmetönung der vitalen oxydationsvorgänge in Eiern. *Biochem. Zeitschr.*, 35: 246-328.
- MICHAELIS, L., and SMYTHE, C. V. 1938. Biological oxidations and reductions. *Annual Rev. Biochem.*, 7: 1-36.
- MORAN, T. 1925. The effect of low temperature on hen's eggs. *Proc. Roy. Soc. B.*, 98: 436-456.
- MORGAN, T. H. 1895. Studies of the 'partial' larvae of *Sphaerechinus*. *Arch. Entw.-mech.*, 2: 81-126.
- . 1901. The proportionate development of partial embryos. *Arch. Entw.-mech.*, 13: 416-435.
- . 1903. The gastrulation of the partial embryos of *Sphaerechinus*. *Arch. Entw.-mech.*, 16: 117-124.
- MORGULIS, S. 1911. Studies of inanition and its bearing upon the problem of growth. *Arch. Entw.-mech.*, 32: 169-268.
- NEEDHAM, J. 1931. Chemical Embryology. Cambridge University Press.
- . 1933. On the dissociability of the fundamental processes in ontogenesis. *Biol. Rev.*, 8: 180-223.
- NORTHROP, J. H., and HERRIOTT, R. M. 1938. Chemistry of the crystalline enzymes. *Annual Rev. Biochem.*, 7: 37-50.
- OSBORNE, T. B., and MENDEL, L. B. 1914. The suppression of growth and the capacity to grow. *Jour. Biol. Chem.*, 18: 95-106.
- , and —. 1915. The resumption of growth after long-continued failure to grow. *Jour. Biol. Chem.*, 23: 439-454.
- PARKER, R. C. 1936. The cultivation of tissues for prolonged periods in single flasks. *Jour. Exp. Med.*, 64: 121-130.
- . 1938. Methods of Tissue Culture. Hoeber, New York.
- PARKS, G. S., and HUFFMAN, H. M. 1932. The Free Energies of Some Organic Compounds. Chem. Catalog. Co., New York.
- PASTEELS, J. 1934. Recherches sur la morphogénèse et le déterminisme des segmentations inégales chez les Spiralia. *Arch. d'Anat. Microsc.*, 30: 161-197.
- PÜTTER, A. 1911. Vergleichende Physiologie. Gustav Fischer, Jena.
- QUASTEL, J. H., and WHETHAM, M. D. 1924. The equilibria existing between succinic, fumaric and malic acids in the presence of resting bacteria. *Biochem. Jour.*, 18: 519-534.
- RAHN, O. 1932. Physiology of Bacteria. Blakiston, Philadelphia.
- RANZI, S. 1931. Sviluppo di parti isolate di embrioni di Cefalopodi. (Analisi sperimentale dell'embriogenesi). *Pubb. Stas. Zool. Napoli*, 11: 104-146.
- RAPKINE, L. 1931. Sur les processus chimiques au cours de la division cellulaire. *Ann. de Physiol. et de Phys.-Chem. Biol.* 7: 382-418.
- RAYLEIGH, Lord. 1896. The Theory of Sound. 2nd ed. MacMillan, London.
- . 1915. The principle of similitude. *Nature*, 95: 66-67 and 202 and 644.

- RICHARDS, A. 1935. Analysis of early development of fish embryos by means of the mitotic index. *Amer. Jour. Anat.*, 56: 355-408.
- ROSE, W. C. 1938. The nutritive significance of the amino acids. *Physiol. Rev.*, 18: 109-136.
- ROWNTREE, L. G. 1936. The role of the thymus gland in growth and development. *Trans. Assoc. Amer. Physicians*, 51: 148-160.
- RUBENSTEIN, B. B., and GERARD, R. W. 1934. Fertilization and the temperature coefficients of oxygen consumption in eggs of *Arbacia punctulata*. *Jour. Gen. Physiol.*, 17: 677-686.
- RUNNSTRÖM, J. 1928. Zur experimentellen Analyse der Wirkung des Lithiums auf den Seeigelkeim. *Acta Zool.*, 9: 365-424.
- . 1930. Atmungsmechanismus und Entwicklungserregung bei dem Seeigellei. *Protoplasma*, 10: 106-173.
- . 1935. On the influence of pyocyanine on the respiration of the sea-urchin egg. *Biol. Bull.*, 68: 327-334.
- . 1937. Die physikalischen chemischen Grundlagen der Protoplasmastruktur und des Stoffwechsels. *Fortschritte d. Zool.*, 2: 251-269.
- RYAN, F. J. 1941a. Temperature change and the subsequent rate of development. *Jour. Exp. Zool.*, 88: 25-54.
- . 1941b. The time-temperature relation of different stages of development. 81: 431-440.
- SCHECHTER, V. 1937. Calcium reduction and the prolongation of life in the egg cells of *Arbacia punctulata*. *Biol. Bull.*, 72: 366-376.
- SCHMIDT, H. 1904. Zur Kenntnis der Larvenentwicklung von *Echinus microtuberculatus*. *Verh. Phys.-med. Ges. Würzburg*, 36: 297-336.
- SEARER, C. 1922. On the heat production and oxidation processes of the echinoderm egg during fertilisation and early development. *Proc. Roy. Soc. B.*, 93: 410-425.
- SLIVER, E. H. 1932. Insect development. IV. External morphology of grasshopper embryos of known age and with a known temperature history. *Jour. Morph.*, 53: 1-22.
- SMITH, P. E. 1916. The effect of hypophysectomy in the early embryo upon the growth and development of the frog. *Anat. Rec.*, 11: 57-64.
- SPEMANN, H., and BAUTZMANN, E. 1927. Über Regulation von Tritonkeimen mit überschüssigem und fehlendem medianem Material. *Arch. Entw.-mech.*, 110: 557-577.
- , and FALKENBERG, H. 1919. Über asymmetrische Entwicklung und Situs inversus viscerum bei Zwillingen und Doppelbildungen. *Arch. Entw.-mech.*, 45: 371-422.
- SPENCER, H. 1898. The Principles of Biology. Revised ed. Appleton, New York.
- TANG, P. 1933. On the rate of oxygen consumption by tissues and lower organisms as a function of oxygen tension. *QUART. REV. BIOL.*, 8: 260-274.
- TEISSIER, G. 1929. La croissance embryonnaire de *Chrysaora hysocella* (L.). *Arch. de Zool. exp. et gen.*, 69: 137-178.
- THOMPSON, D'ARCY, W. 1915. The principle of similitude. *Nature*, 95: 202-203.
- . 1915. Galileo and the principle of similitude. *Nature*, 95: 426-427.
- . 1917. Growth and Form. Cambridge University Press.
- THOMPSON, H. B., and MENDEL, L. B. 1917. An experimental study of alternating growth and suppression of growth in the albino mouse, with special reference to the economy of food consumption. *Amer. Jour. Physiol.*, 45: 431-460.
- TOLMAN, R. C. 1914. The principle of similitude. *Physical Rev.* 3: 244-555.
- TYLER, A. 1933. On the energetics of differentiation. A comparison of the oxygen consumption of "half" and whole embryos of the sea-urchin. *Publ. Stas. Zool. Napoli*, 13: 155-161.
- . 1935. *Ibid.* II. Comparison of the rate of development of giant and normal sea-urchin embryos. *Biol. Bull.*, 68: 451-460.
- . 1936a. *Ibid.* III. Comparison of the temperature coefficients for cleavage and later stages in the development of the eggs of some marine animals. *Biol. Bull.*, 71: 59-81.
- . 1936b. *Ibid.* IV. Comparison of the rates of oxygen consumption and of development at different temperatures of eggs of some marine animals. *Biol. Bull.*, 71: 82-100.
- . 1937. *Ibid.* V. Comparison of the rates of development and of oxygen consumption of tight membrane and normal echinoderm eggs. *Jour. Exp. Zool.*, 76: 395-406.
- . 1939. Crystalline echinochrome and spinochrome: Their failure to stimulate the respiration of eggs and of sperm of *Strongylocentrotus*. *Proc. Nat. Acad. Sci.*, 25: 523-528.
- , and DESSEL, F. W. 1939. Increasing the life span of unfertilized *Urechis* eggs by acid. *Jour. Exp. Zool.*, 81: 459-472.
- , and HUMASON, W. 1937. On the energetics of differentiation. VI. Comparison of the temperature coefficients of the respiratory rates of unfertilized and of fertilized eggs. *Biol. Bull.*, 73: 261-279.
- , and HOROWITZ, N. H. 1938a. *Ibid.* VII. Comparison of the respiratory rates of parthenogenetic and fertilized *Urechis* eggs. *Biol. Bull.*, 74: 99-107.
- , and —. 1938b. The activities of various substituted phenols in stimulating the respiration of sea-urchin eggs. *Biol. Bull.*, 75: 209-223.

- TYLER, A., RICCI, N., and HOROWITZ, N. H. 1938. The respiration and fertilizable life of *Arbacia* eggs under sterile and non-sterile conditions. *Jour. Exp. Zool.*, 79: 129-143.
- , and SCHEER, B. 1937. Inhibition of fertilization in eggs of marine animals by means of acid. *Jour. Exp. Zool.*, 75: 179-197.
- , and SCHULTZ, J. 1932. Inhibition and reversal of fertilization in the eggs of the echiuroid worm *Urechis caupo*. *Jour. Exp. Zool.*, 63: 509-532.
- VOEGTLIN, C., MAVER, M. E., and JOHNSON, J. M. 1933. The influence of oxygen tension on the reversal of proteolysis (protein synthesis) in certain malignant tumors and normal tissues. *Jour. Pharmacol. Exp. Therap.*, 48: 214-265.
- WADDINGTON, C. H. 1932. Experiments on the development of chick and duck embryos, cultivated in vitro. *Phil. Trans. Roy. Soc. B.*, 221: 179-230.
- WARBURG, O. 1908. Beobachtungen über die Oxiationsprozesse im Seeigellei. *Zeitschr. physiol. Chem.*, 57: 1-16.
- . 1915. Notizen zur Entwicklungsphysiologie des Seeigelleies. *Arch. f. ges. Physiol.*, 160: 324-332.
- . 1937. Chemische Konstitution von Fermenten. *Ergeb. Enzymforsch.*, 7: 210-245.
- WATERS, H. J. 1908. The capacity of animals to grow under adverse conditions. *Proc. Soc. Prom. Agr. Sci.*, 29: 71-96.
- WEISS, P. 1939. Principles of Development. Henry Holt, New York.
- WHITAKER, D. 1933. On the rate of oxygen consumption by fertilized and unfertilized eggs. V. Comparison and interpretation. *Jour. Gen. Physiol.*, 16: 497-528.
- . 1937. Extension of the fertilizable life of unfertilized *Urechis* eggs by alcohol and by dextrose. *Jour. Exp. Zool.*, 75: 155-167.
- WIGGLESWORTH, V. B. 1936. The function of the corpus allatum in the growth and reproduction of *Rhodnius prolixus* (Hemiptera). *Quart. Jour. Micr. Sci.*, 79: 91-122.
- WOODGER, J. H. 1930. The "Concept of Organism" and the relation between embryology and genetics. Parts I & II. *QUART. REV. BIOL.*, 5: 1-22 and 438-463.
- . 1931. The "Concept of Organism" and the relation between embryology and genetics. Part III. *QUART. REV. BIOL.*, 6: 178-207.
- WOODS, E. 1925. Some observations upon the role of cystine and certain mineral elements in nutrition. *Jour. Biol. Chem.*, 66: 57-62.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of The Quarterly Review of Biology, Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore, Maryland, U. S. A.

NATI SUNT MURES, ET FACTA EST CONFUSIO
Being a review of *Voles, Mice and Lemmings: Problems in Population Dynamics*, by Charles Elton. (Oxford University Press, New York: Clarendon Press, Oxford, 1942. Pp. 496.) By G. Evelyn Hutchinson, Yale University.

The name of Elton has been associated with studies on populations of small mammals for nearly twenty years and it is therefore with eagerness that an ecologist takes up this monumental volume which, produced after two years of war, still maintains in its material aspects the distinction to be expected of its publishers. Here, hidden in close to five hundred pages of text, must lie the secret of the lemmings and in this great work we may hope to find exposed the working of that strange metronome that seems to regulate the animate beings of arctic lands. A first reading, however, leaves a sense of disappointment; in spite of the continuous activity of Elton and his associates, he can only "begin to see vole populations in dynamic terms: with numbers, rates of increase, life-curves, and movements interwoven into a pattern that ten or twenty years' further work may enable us to understand completely." All this immense labor is then preliminary, is the reconstruction of the historic background, the elaboration of technique. The main investigation has yet to come. Meanwhile, every student of animal population will be grateful for these studies, which provide the most comprehensive existing body of data on the periodic fluctuations of any group of animals.

The book is divided into four parts. The first is a review of previous work on murid populations, in Central Europe, the Soviets, North America, and certain other parts of the world. The effects of biological control, in France particularly, are considered; the summary of the Russian investigations is most illuminating; Hamilton's studies are naturally regarded the most significant contributions from the United States. The second part is devoted to Britain and Scandinavia, and deals with the work of Elton's own Bureau of Animal

Populations at Oxford and with the Norwegian lemming. The whole of the rest of the book is devoted to an immensely detailed account of the periodicities found in northeastern arctic Canada, Part 3 being limited to northern Labrador, Part 4 to Ungava. No detail that might be relevant seems to be omitted; everything cognate to the subject is here, the shiny leaves of the mountain laurel, the starving Indian, the apt quotation from Bridges. Yet on page 482, after a discussion of epidemic diseases in sledge-dogs, the work suddenly ends with an allegory of nine lines. A few more facts are added in an appendix and the volume completed with a somewhat unsatisfactory index. The final section, the integration of the material that might have been expected, is nowhere to be found; the war may have prevented a concluding section from being written, but the whole tenor of the work suggests that Elton prefers each reader to construct mentally such a chapter for himself. This is a difficult task, particularly for the reviewer, who must think publicly. Like some aboriginal woodman who has learned to know intuitively the whole puzzling geography of an immense forest, Elton finds his way easily through thick undergrowth of detail, without any intellectual map to guide him. The less practiced reader must digress to set the problems somewhat more abstractly than his guide is willing to do.

The fundamental question can be expressed simply enough. In many parts of the world small rodents multiply, becoming excessively numerous, and often very destructive, in certain years, after which the population suddenly declines. These increases may appear sporadically, but usually there is a clear indication of periodicity in any given locality, and in almost every region where the matter has been studied, the interval between maxima tends to be three to four years. The problem we must set ourselves is to ascertain the causes of this periodic increase and decline.

In constructing an intellectual map as a guide to the possible solutions of the problem we may first notice

that, if the numbers of any animal depend on the reproductive potential of the population of the preceding generation and on the environmental resistance, and if the reproductive potential of the individual is considered constant while the environmental resistance fluctuates with the meteorological conditions, we shall have a fluctuating population. Any given departure from the mean meteorological conditions will have, in any locality, a definite probability of occurrence, and if no secular changes are occurring in the climate, the departure in one year is independent of the departure in any other. As we suppose that both climate and number of parents available determine the population, the occasional chance appearance of "runs" of favorable or unfavorable meteorological conditions will permit the building up of large populations, or cause progressive declines. Over a long period of time the mean interval between such maxima or minima will tend to the same value as the mean between maxima or minima observed over another long period, or in another locality, where the frequency distribution of meteorological probabilities is the same. This principle we shall call *statistical quasiperiodicity*. It introduces a note of caution into all work on animal numbers; many of the less regular periodicities, such as the so-called 5-7 year cycle in partridge and grouse in Great Britain, may be of such a kind. Elton's data on the voles clearly represent something more regular than this.

If we have a real periodicity, it may presumably be due to cyclical events outside the ecosystem or to the generation of cycles by mechanisms inside the biological system, the former condition corresponding to forced vibrations in mechanics, the latter to free vibrations. In the case of two isolated but climatically and geographically close populations of an animal, if the periodicity is externally determined or forced, the fluctuations in the two populations may reasonably be expected to be synchronous. In more remote regions, the oscillations might show a constant phase difference, but any irregularities in one region should correspond to irregularities in another. If the oscillation is free, there is no reason why the two populations should fluctuate in phase or with correspondence in their irregularities. The exact number of possible ways in which free fluctuations may occur is hard to ascertain *a priori*, but most cases probably reduce formally either to the symmetrical, so-called *classical oscillations* involved in the *prey-predator* relationship (Lotka-Volterra periodicity, developed in a different form by Nicholson and Bailey) or to the *relaxation oscillations* of Gause. Gause's theory involves the building up of the population to a certain critical level, after which it becomes unstable and declines suddenly, the most obvious causes of the decline being exhaustion of food, or abnormal opportunities for the spread of epidemics, when the critical density is reached. A final word of warning is needed; it is tempting to suppose a multiple causality, and this is no doubt correct, but it is clear that one must not

postulate interaction of periodic causes with different periods, not multiples of each other, and then hope to obtain a highly regular set of maxima. This has been done in the past by authorities who should have known better.

The facts that Elton and his predecessors appear to have determined are these:

(a) Over large tracts of land the periodicities often appear to be synchronous; this is the case over northern Labrador and Ungava. But when northern Labrador and Norway are considered, Elton, who formerly believed synchronism to exist, now merely states that he had hoped to make a comparison; although no such comparison apparently is made in the text, it is easy to see that there is no evidence for an identity in phase. This, however, does not exclude synchronism altogether, because the best data for comparison relate to a derived element, the number of foxes killed, and the maxima in foxes may either *coincide with* or follow by *one year*, the maxima in lemmings and voles. Casual examination, without detailed statistical analysis, suggests to the reviewer that it is actually very unlikely that the maxima of the primary population of rodents are in phase in the New and Old Worlds. Further analysis of the distribution in the two series of abnormally long or short periods (3 or 5 years) might, however, be made. In spite of the huge distances involved in Labrador and Ungava it is uncertain that a synchronism significant in separating internal from external causation, can be established on a continuous land mass. In Great Britain, and in Bavaria, moreover, cycles are known in different *Microtus* populations, all fairly regular, but not in phase.

(b) The periodic appearance of Microtinae as major influents in any eco-system, naturally alters all the trophic dynamics of that system. In Norway and the Canadian arctic there is a shift in food habits of predators whenever the maxima occur, releasing the pressure on other species. Any argument based on co-occurrence of cycles in non-predatory animals in the same region may therefore be as irrelevant to the problem of internal versus external control, as is the increase in foxes when the lemmings increase. It must also be observed that the predatory carnivores, known so well from the statistics of the fur trade, are not involved in generating a Lotka-Volterra cycle with the rodents, for the latter fluctuate after man has decimated the population of carnivorous mammals. Moreover it may be noted, though it has apparently not been pointed out in print, that if the expression for the approximate period, given by Volterra, be used in the case of the snowshoe rabbit and its principle predator, we obtain an absurd expectation of life for a starving lynx.

(c) Although the curves indicating the numbers of predators killed (or in other cases, the actual numbers of cyclical rodents, such as *Lepus americanus*), show, when based on data derived from large areas, reasonably symmetrical maxima and minima, this symmetry is

probably largely due to the superposition of a number of asymmetrical curves, some being slightly out of phase. Everyone who has studied the matter carefully concludes that at a given station the decline in the primary fluctuating population is rapid and asymmetrical. Moreover, the animals with a 3-4 year cycle are apparently all annuals, and there is a critical period each spring when the whole breeding population consists of middle-aged individuals with a relatively low expectation of life, as Leslie and Ranson, of the Oxford Bureau of Animal Population, have shown. The existence of this critical period, should any postponement of suitable breeding conditions occur, may be disastrous, and is therefore one of the most important properties of the life history of voles. Of itself, however, the critical period does not explain periodicity.

(d) Though analysis of field records suggests a picture not unlike Gause's relaxation oscillation, no clear evidence of epidemic disease as the controlling factor exists. In some declines in Britain, the Oxford workers found *Toxoplasma* infections more or less epidemic; in other cases the most careful pathological study failed to reveal any general morbidity in the population. A form of tuberculosis is occasionally reported, and though its incidence is of great pathological interest, there is no evidence that this disease plays any part in the regulation of cycles. Certain interesting facts relating to the age distribution of infection by annual parasites also came to light in the Oxford studies, but do not bear on the main problem.

(e) Hamilton's work suggests a great rise in fertility as the numbers increase. This is in part due to sexual undercrowding or reduction of encounters between the sexes, at the minimum, but at that time the breeding season is shorter, and the number of young per litter lower, than in the later parts of the period of recovery. Unless the reduction in fertility actually intervenes in a still more extreme form, immediately prior to the decline, we cannot interpret cyclic changes in population in terms of cyclic change in reproductive potential, for, at the minimum, the population has ceased to decrease and is about to increase. Elton summarizes some evidence that overcrowding causes an excessive incidence of combats, both between males and between females; this may induce an increased mortality and conceivably might result in low fertility and so, in view of the critical period in the spring, cause a decline. Such social antagonisms can hardly be the explanation of the low litter number, per fertile mating, at the minimum. Hamilton thinks that such variation in fertility is a phenomenon general in small rodents; the limited investigations of Elton's associates seem to indicate that in *Microtus agrestis* there is less reproductive variability than in the American forms. The problem of fertility is clearly of the greatest importance, and its solution might throw light on some of the obscurer aspects of human reproduction.

(f) Something can be learned from comparisons with

other cyclic animals; this, however, is hardly attempted by Elton in the present volume. Though the trophic control of the ecosystem by a four-year microtine cycle is most marked in the northern Tundra, there is no reason to suppose that the ten year cycle of the Canadian forest zone, based on the fluctuation of the numbers of the snowshoe rabbit, is a latitudinal matter, as the four year cycle appears again in *Microtus* far to the south, in New York. The basis for the difference must lie in the sizes, or more directly, in the lengths of life span, of the major primary consumer (herbivore) in the food chain. This hypothesis is strengthened by the fact that squirrels seem to occupy an intermediate category, with a 5-7 year cycle.

These six generalizations seem to point towards an internal relaxation oscillation of Gause's kind, though the cause of the relaxation is still obscure. In one place Elton suggests that the reaction of the animals on the vegetation may almost approach the classical prey-predator interaction of Volterra, though here the most probable result is likely to be a highly asymmetrical relaxation, as Gause has shown to occur in most cases of natural predation. Yet faced with the extraordinary similarity, if not simultaneity, of the cycles in populations spread over a great part of the northern hemisphere, we find it hard to avoid returning, as indeed Elton does, to some external climatic control. The particular meteorological results that are evoked in the present work are derived by Goldie from a study of the distribution of mean annual pressures over western Europe. Indications of an irregular cycle of about 3.8 years are found in such data. It must, however, be admitted that Goldie's period is but one member, and apparently not a very respectable member, of a great family of meteorological periodicities and quasiperiodicities. By far the most remarkable biological periodicities known are derived from the studies of Douglass and his associates on tree growth; here there is no possibility of the cycle being free. Moreover, since there is fairly good evidence that the growth of comparable Miocene trees and other ancient annual phenomena of variable intensity, behaved essentially like modern trees in the frequency of appearance of any given cycle, it appears that the cycles, though they come and go irregularly, have definite probabilities of occurrence, and are therefore *real*, and, being independent of the present detailed distribution of land and water, are presumably *solar*. Different groups of trees show certain cycles more intensely than other groups, so that we may regard the system "tree + climatic environment" at any place as resonating to certain periods in the extremely complex meteorological rhythmicity of the whole atmosphere. If animal populations behave in the same way, the length of the life cycle may perhaps determine the period of resonance. But this is a flight into theory further than our author would permit us; let us therefore wish him a speedy return to his inter-

rupted studies, so that, after many mice have been born, we may, in ten or twenty years, have a companion

volume in which the confusion that now permeates the whole subject will be resolved into order.

BRIEF NOTICES

EVOLUTION

THE EXTREMITY BONES OF SINANTHROPUS PEKINENSIS. *Palaeontologia Sinica, New Series D, No. 5; Whole Series No. 116.*

By *Frans Weidenreich. Geological Survey of China, Peking.* 11½ x 8½; 150 + 34 plates. 1941 (paper). Our knowledge of early man has been greatly advanced by the important discovery of the remains of *Sinanthropus* near Peking. These significant finds have been described in a series of exemplary monographs by the late Davidson Black and more recently by Professor Weidenreich. The previous reports were devoted chiefly to skulls and teeth which, curiously enough, had been preserved in larger numbers than other skeletal parts. The present contribution deals with the few extremity bones of *Sinanthropus* found so far. These comprise seven incomplete thigh bones, two fragments of upper arm bones, one incomplete collar bone, and one wrist bone (lunatum). All these specimens are from adult individuals and, with only one exception, from males according to the most probable sex determination. Unfortunately all the long bones lack their joints, only more or less extensive portions of the shafts having been preserved. Practically no doubt is left that these limb bones really belong to the same type of early man as the previously recorded skulls and teeth. These scanty, yet most welcome and encouraging finds appertaining to the limbs of *Sinanthropus* are described in very careful and adequate detail. Humerus, femur and clavicle have been reconstructed so that at least their total lengths can be estimated with a fair degree of confidence. They are compared meticulously with the corresponding bones of other fossil men, of modern man and of the man-like apes in regard to their main proportions and their most significant descriptive characters.

Of the conclusions the following are specially noteworthy: In all their main features these extremity bones are practically identical with those of modern man and show none of the conditions characteristic of the apes. This is highly interesting and quite surprising in view of the many primitive or at least peculiar conditions found in the skulls. As a distinctive trait of *Sinanthropus* is mentioned that in the femur and the humerus the medullary canal is strikingly narrow and the walls of the shafts are correspondingly thick. Weidenreich considers it safe to conclude that *Sinanthropus* had already assumed a completely upright posture. He estimates the stature of this fossil man at approximately 156 cm. in the male and 144 cm. in the female.

In an appendix the author discusses the precise nature and the probable causes of "the fragmentariness

of the extremity bones." Here it is concluded that apparently "carnivores and man competed in the breaking of bones both human and animal." In his introduction Weidenreich sides in principle with that steadily growing number of scientists who are dissatisfied with the present, often misleading and certainly inconsistent, nomenclature applied to the various forms of man. Even though we have undoubtedly been far too generous in bestowing so many different generic names to our nearest fossil relations, it is startling to read the author's confession: "I believe . . . that all known hominids belong to one-and-the-same species." Let us hope that the fashions in the taxonomy of the Hominidae will not swing from one extreme to the opposite!



A MIOCENE SEA LION FROM LOMITA, CALIFORNIA. *University of California Publications in Zoology, Volume 47, No. 2.*

By *Gretchen M. Lyon. University of California Press, Berkeley and Los Angeles.* 10½ x 6½; 30 + 6 plates; 1941 (paper).



GENETICS

AMERICAN DAIRY CATTLE: *Their Past and Future.*

By *E. Parmelee Prentice. With Chapters on Dairy Cattle in America by Ernest L. Anthony, Lloyd Burlingham, Clifford Clevenger, and Others. Harper and Brothers, New York and London.* \$3.00. 9½ x 6½; xix + 453; 1942.

This excellent and colorful volume presents in a clear and authoritative manner the history of the development of our Holstein, Jersey, Shorthorn, Guernsey, Ayrshire, and Brown Swiss breeds of American dairy cattle. In addition to the time-worn histories and encyclopedias usually used for research, the author of this work has availed himself of another very valuable source of data relating to the history of cattle; namely, the Port and Custom House records of Britain, and the contemporary advertisements in *The Times*. The result is a fascinating history of one of the most intriguing facets of man's progress.

The history of cattle is really the history of man, inasmuch as they have shared his struggle for existence and at the same time have contributed materially to his welfare. Although cattle were tended and were used for their meat and dairy products from the earliest days of recorded history, their purposeful breeding had

its origin in England during the 17th Century. There, under the impetus of three factors (the need for more food for man, the importation of Dutch cattle, and the increase in supply of agricultural products which could be used for cattle food) the random crossing of native stocks began. Animals which were fed and bred into greatness became a breed. Of course there was no knowledge at that time of the laws of inheritance, so that acquired characters, maternal impressions, and many other outside influences were thought to affect the character of the offspring. Thus, importance was soon attached to cattle from a certain locality, or to those being bred by a particular man who was able to keep his stock well fed. This was essentially the picture of cattle production up to the beginning of the present century, when, in America, under the impetus of increased knowledge of heredity and the institution of the dairy breed herd book, the all-important factor became the lineage of the stock—lineage without reference to production qualities. In the past decade, with the collection of detailed production records and the application of statistical methods, the progeny test (which takes into account the productive ability of the progeny, and which holds that this is even more important than lineage) has been established and is accepted as the last word in method of live stock improvement. From the recent production records of cattle selected by the progeny test method, no one can even hazard a prediction as to how far the development and improvement of dairy cattle can, and will, go.

For anyone interested in live stock production and improvement, this history of cattle will prove as fascinating as it is informative. The text is profusely illustrated and is supplied with a detailed index.



METHODS OF PLANT BREEDING.

By Herbert Kendall Hayes and Forrest Rhinehart Immer. McGraw-Hill Book Company, New York and London. \$4.00. 9 x 6; xii + 432; 1942.

This new book is an excellent addition to the literature at the disposal of students of agriculture and plant breeding who are familiar with the elements of genetics. It is predominantly concerned with problems of practical breeding. However, the importance of genetic and cytogenetic principles is emphasized throughout the book.

The greatest part of the book is devoted to the description and critical evaluation, from both the theoretical and practical standpoints, of the general principles and methods of modern plant breeding. A brief discussion of the genetic and cytogenetic basis of plant breeding is followed by chapters concerned with the mode of reproduction in relation to breeding methods, technics of selfing and crossing, the pure line method of breeding naturally self-pollinated plants, the back-cross method, hybridization as a method of improving

self-pollinated plants. These are supplemented by special chapters concerned with the breeding of some economically important plants: wheat, oats, barley, flax and corn; with controlled pollination methods of breeding cross-pollinated plants and seed production; and by a thorough discussion of statistical methods used in plant breeding.

The text is accompanied by 20 pages of bibliography, a glossary and statistical tables.



NEW PATHS IN GENETICS.

By J. B. S. Haldane. Harper and Brothers, New York and London. \$2.50. 8½ x 5½; 206; 1942.

In introducing this new book to the non-professional reader, the author shows that the present day geneticist "must be a jack of all trades and it is to be feared that he may become the master of none" (p. 15). That the latter is not a necessary corollary of the former is exemplified by the author himself who, in a series of lectures delivered at the University of Gröningen and now published in bookform, not only treats with great competence the various aspects of genetics, but also amply quotes his own contributions in the diverse fields of this science.

The first chapter (The science of genetics) is devoted to a general review of the field of genetics. The relations of genetics to biochemistry and embryology are discussed in the next two chapters (Genetics and biochemistry, Genetics and development), while the last two chapters (The genetics of some human abnormalities, The formal genetics of man) are specially concerned with human genetics.

The book, written in a clear but not wholly unpretentious style, will be read with equal interest by students of genetics, embryology, biochemistry and medicine.



SEVEN PAPERS IN GENETICS AND PHYSIOLOGICAL GENETICS OF DROSOPHILA MELANOGASTER. University of California Publications in Zoology, Volume 49, Nos. 1-7

By Richard Blanc, Werner Braun, Eldon J. Gardner, Richard Goldschmidt, Claude A. Villee, Jr. University of California Press, Berkeley. \$2.00. 10½ x 6½; 184 + 11 plates; 1942 (paper).

This volume, under the general title *Seven papers in Genetics and Physiological Genetics of Drosophila melanogaster*, contains the following articles: Observations on the production of wing scalloping in *Drosophila melanogaster*, by Richard Blanc; Phenocopies and X radiation in *Drosophila melanogaster*, by Richard Blanc and Werner Braun; The effect of X-radiation upon bristle pattern in *Drosophila melanogaster*, by Richard Blanc and Claude A. Villee, Jr.; The effect of changes in time development on the phenotype of mutants of *Drosophila*

melanogaster, by Werner Braun; A further study of genetic modification of dominance, especially by position effects, by Eldon J. Gardner; A further contribution to the analysis of scalloped wings in *Drosophila melanogaster*, by Richard Goldschmidt and Eldon J. Gardner; A study of hereditary homoeosis: the mutant tetraltera in *Drosophila melanogaster*, by Claude A. Villee, Jr.



A REPORT ON EXPERIMENTS WITH COLCHICINE by Laymen Scientists during 1941. A Co-operative Research Project.

By O. J. Eigsti and Barbara Tenney. University of Oklahoma Press, Norman, Oklahoma. 35 cents. 9 x 6; 32; 1942 (paper).

This pamphlet is a report of a project designed to encourage laymen to carry out experiments with colchicine (by its use polyploidy may be produced). Colchicine along with directions for an experiment with it were sent to a group of laymen who were then requested to turn in a report on their work. The present pamphlet describes the nature of the project, gives some facts about colchicine, gives the details of the carrying out of the project, analyzes the geographic distribution and occupations of the experimenters, and summarizes the results of the reports. Successful induction of changes was reported in 19.4 per cent of the completed experiments or in 7.1 per cent of the total number of experiments. Over 60 per cent of the experiments were not reported or incomplete. The authors conclude that the use of colchicine by laymen is not of great economic value but is a valuable method of education. From the fact that 51 per cent did not send in a report it would seem that it also shows how difficult it is to keep laymen interested in such a project.



BIOLOGICAL SYMPOSIA. Volume VI. I. Temperature and Evolution. II. Isolating Mechanisms. III. Genetic Control of Embryonic Development.

Edited by Th. Dobzhansky. The Jaques Cattell Press, Lancaster. \$3.50. 9½ x 6½; xii + 355; 1942.

This sixth volume of the series of Biological Symposia contains papers read by fifteen authors at three different symposia. The subjects of these were: Temperature and evolution; Isolating mechanisms; Genetic control of embryonic development. In the first two the emphasis is on the evolutionary aspects of the problems, the third one is a further attempt to bridge the gap between embryology and genetics. Thus this volume is another manifestation of the continually growing interest of geneticists in correlating their particular field with general biological theory.

The volume is edited and prefaced by Th. Dobzhansky.

GENERAL BIOLOGY

UNIVERSITY OF COLORADO STUDIES. Series D. Physical and Biological Sciences, Vol. I, No. 4. Containing the following: *Vegetation of the San Luis Valley in Southern Colorado*, by Francis Ramaley; *Alphabetical Index to Volume 1 of Series D (Physical and Biological Sciences)*; *Title Page and Contents*.

University of Colorado, Boulder, Colorado. \$1.00. 10 x 6½; 231-279; 1942 (paper).



HUMAN BIOLOGY

TIME AND THE PHYSICIAN. *The Autobiography of Lewellys F. Barker.*

By Lewellys F. Barker. G. P. Putnam's Sons, New York. \$3.50. 9 x 6; ix + 350. 1942.

Due, perhaps, in greatest measure to the changes in mores which marked the decline of aristocracy and the rise of the proletariat, writers of autobiographies of late years have exercised a restraint in frankness, absent in the autobiographies of Cellini, Casanova, Rousseau, and Franklin, and in the letters and diaries of men and women of the 17th and 18th centuries, which revealed so vividly and so fully their real natures and portrayed the spirit of the times in which they lived, moved, and had their being. From such as these we get clear-cut pictures of the individual scribes, their associates, and their general milieu. In this natural frankness which flourished before the reign of Mrs. Grundy, the stepdaughter of the "puritan" sects and the godmother of the Comstocks, lies much of the charm these writers exert upon intelligent students of human nature. The same criticism applies, with certain notable exceptions, to biographers. Fortunately, in the novel, which deals in essence with the biographies of imaginary persons, authors have to a considerable degree escaped the fetters of a false prudery.

Beyond the members of the other learned professions, accounts of the accomplishments and descriptions of the personalities of successful medical men possess a wider popular interest. Doctor Barker is in eminent degree a successful medical man in scientific attainments, in teaching, in diagnosis, and in therapy. In addition, he is a man of unusual charm; his activities have covered many countries and climes; his interests are broad and deep; his ideals are high. By dint of hard labor, self-denial, and a peculiar perspicacity in the choice and direction of his studies, he so cultivated his natural gifts that he early attained eminence in several branches of his chosen calling. Barker's early training in chemistry, anatomy, physiology, general pathology, pathological anatomy, and bacteriology, and especially in neurology and psychology, gave him a unique background for the study, teaching, and practice of clinical medicine. His clinical lectures given in the amphitheatre, were prepared with the care and thoroughness

which characterized those of certain great clinical teachers of earlier generations of whom Da Costa of Philadelphia and Trousseau of Paris are pertinent examples.

In the study and care of private patients, occupying his later life, Barker has considered the individual as a whole; the man, himself, as an integrated organism. Penetrating beneath the subjective symptoms and the pathological processes disclosed by exhaustive investigation with the aid of methods and techniques of precision, he has sought to obtain that comprehensive insight into all the factors involved, which is so essential for accurate diagnosis and intelligent therapy.

The author's avowed intent is an honest attempt to dissect and to evaluate his own personality as influenced by heredity and environment, personal and physical. The result is a book well written and readable withal; but in the opinion of this reviewer, undue space is given to narrative of travel and to hero worship of teachers and colleagues, the more important of whom have been already exhaustively written about.

Despite his keen and penetrating mind, and his wide reading, influenced unduly perhaps by his early associations, Barker confesses allegiance to the current Christian (*sic*) mores, to belief in a very broad type of democracy, and to adherence to the "uplift."

To the next candidate to autobiography, this reviewer recommends perusal of those of Franklin and Marion Sims.

The clear-cut photograph used as frontispiece, reveals to the amateur physiognomist much of the author's character, especially his earnest determination and the charm that has endeared him to so many in all walks of life.



THE BIOLOGY OF THE NEGRO.

By Julian H. Lewis. University of Chicago Press, Chicago. \$5.00. 9 x 6; xvii + 433; 1942.

The author, who is Associate Professor of Pathology at the University of Chicago, has undertaken the arduous and much needed task of collecting and reviewing a very large part of the most significant and heretofore widely scattered literature appertaining to Negro biology. The resulting volume will be highly welcomed by medical men, anthropologists and sociologists, but it must be judged as a pioneering effort hampered by several basic difficulties. The latter are connected with the precise definition and proper limitation of the subject and fall chiefly under three headings: (1) Does the term "Negro" represent a biological entity? (2) What share of the "Negro" peculiarities discussed is due to real and hereditary qualities and what share is caused chiefly by environmental factors of an economic or sociological nature? (3) Can any one scientist to-day be equally well at home in the many branches of biology so that a work of this sort does equal justice to the many different

subjects dealt with? Regarding the term "Negro" the author states in his preface:

In this book the American usage is followed in review of the American literature, and for other literature only that is used pertaining to the Negroid people of the east and west coasts of Africa and of central and southern Africa as well as the intermixtures called 'colored' by the English. It is confessed that this word 'race' is used very loosely . . .

It is evident that the collected information does not appertain to pure stock, but must frequently refer to variously mixed groups and this even in the case of reports from Africa. Regarding the above second question it can here be merely mentioned that for a great many of the diseases discussed it has to be left undecided to what extent nature or nurture is responsible for apparent racial peculiarities. The table of contents supplies a partial answer to the third question raised. There are chapters on Population and vital statistics (17 pages), on Anatomy (64 pages), and on Biochemical and physiological characteristics (17 pages); the remaining 308 pages of text are devoted to a discussion of different diseases, i.e. to what the author proposes to call "anthropathology" (in the reviewer's opinion an inadmissible term). It is readily seen that the normal conditions are not nearly as well represented as are the morbid ones. This discrepancy is based to some extent and quite naturally upon the fact that the author's chief interest and experience lies in racial pathology and that hence this subject is discussed much more fully than the other fields of biology (psychology is not even mentioned). It must also be recalled, however, that there exists a real and marked difference between the total amounts of available information appertaining to normal race characters on the one hand and to racial peculiarities of disease processes on the other hand and this unquestionably for the reason that the number of people working in medicine is several thousand times greater than the total of investigators in all the different fields of normal human biology.

As a volume which reviews for the first time the enormous accumulation of data bearing upon the characteristics in the Negro's reactions to disease this book belongs in every medical library. Of the positive findings few permit, as yet, broad generalizations. Among the latter the following may here be quoted: "Surgeons who have had considerable clinical experience with Negroes commend them as excellent surgical risks. They are stoic in their reaction to pain and discomfiture, do not easily go into shock, take anesthesia well, resist infection, and show remarkable powers of recovery."

The usefulness of this volume is enhanced by the very adequate subject index and by the author index.



SUN CHIEF: *The Autobiography of a Hopi Indian.*

Edited by Leo W. Simmons. Yale University Press,

New Haven; Oxford University Press, London. \$4.25. 9 x 6; x + 460; 1942.

Those who have idealized the Amerind are due for a rude shock when they read this book. It is not so much the autobiography of a moral degenerate as of a member of a community of moral degenerates. The Hopi Indians are a disappearing tribe and they know it, and are so animated by a philosophy of despair that they have given themselves over wholesale to a life of licentious excesses in which the entire population participates and in which the individual takes pride.

The delinquency of the Indian is popularly attributed to contact with white civilization. In some instances such a conclusion may be justified, for the conduct of the white man in most instances has been far from impeccable. But here we have one who, although exposed to civilization, never caught it, who repudiated a Christianity that he never understood in favor of the superstitious metaphysics of his ancestors, who spent his life in a community where no white person was welcome except the prostitute, yet whose entire career was devoted to pornographic practices, the product of an education that began in the cradle under the expert tutelage of all his female relatives, both natural and ceremonial.

The book was undertaken as a contribution to anthropology. Certainly it contains much that is of anthropological significance. The detailed account of the circumstances of the author's birth indicate how deeply the story was impressed on his consciousness by constant reiteration, and the practices of the medicine men on this as well as on subsequent occasions testify as to the power exercised by these people over their superstitious followers. The stories of his initiation into two secret societies throw light on the cultural heritage of his people, but the high spot in the book is the account of the famous snake dance, including the ritual which takes place within the kiva, of which the ordinary tourist is unaware. This ritual is supposed to be guarded, but it is partly revealed here to correct some misstatements in an earlier published work. One suspects also that a pecuniary compensation was not without influence in eliciting the information.

In the final analysis the greatest significance of this book will probably prove to be as an influence in the refutation of the impractical theory held by sentimentalists that all would be well with the Indian were the activities of missionaries and educators curtailed.

The reviewer's feeling on putting down this book is that the Hopi Indians have undergone considerable deterioration within rather recent years. It is difficult to reconcile the picture of the Hopi character which this narrator gives us with the tradition that makes the Pueblo Indians the most advanced in the Southwest, and the Hopi the noblest among the Pueblos. And the contrast between Sun Chief's picture of himself and the popular conception of some of the more dignified figures in Indian history, such as Logan, Osceola, or Elias

Boudinot is very striking. But then there are many white men who do not measure up to the standard of Thomas Jefferson or Abraham Lincoln.



THE HOUSE IN THE RAIN FOREST.

By Charis Crockett. Houghton Mifflin Company, Boston. \$3.00. 8½ x 5½; x + 300; 1942.

This is an informative anthropological book and at the same time, incredible as it may seem, a charming account of a long honeymoon among the little-known savages of Dutch New Guinea. The author has a degree in anthropology from Radcliffe and, since she really wanted to make good use of her training, she sailed with her husband in a 59-foot schooner through the Panama canal, among the South Sea islands, and to the western end of the land of the Papuans where they lived happily in their house on stilts in the rain forest. In the introduction Professor Hooton states that "the present work is a casual by-product of her contribution to science. Actually she measured nearly 900 greasy, smelly, filthy cannibals—a remarkable achievement for any tough, male physical anthropologist and a miracle for a fragile, blonde female."

Mrs. Crockett succeeded first of all in winning the confidence and even the affection of the really primitive natives among whom she lived. She has also succeeded in giving a delightful, intimate picture of the daily life and the child-like nature of her aboriginal neighbors with their simple ambitions, limited to food and love, their naive superstitions, and their enviably few needs and worries. These natives (*Madik*) were at first shy and timid as well as quite suspicious. Soon, however, *Madik* society trusted and accepted their white visitors, a change that was accelerated, as among most savages, by the readily offered medical aid of the Crocketts. The author admits cheerfully that they found it "far easier to become a successful quack than a competent doctor and we had more luck in treating magical diseases than physical ones."

The Dutch authorities have done their best to eradicate cannibalism at least in the coastal districts, but they have not yet changed the natives' views concerning this culinary subject. According to the author, the *Madik* "were profoundly shocked to hear that in our country a man may contemplate slaughtering and eating his own pig—it indicated a scandalous lack of delicacy and proper feeling. But to waste the nutritive value of a houseful of dead bodies would have seemed to them incomprehensibly silly, wantonly spendthrift." Even though these and many other Papuan ideas and customs appear to be exceedingly primeval and savour decidedly of cavemen's days, these savages enjoy more happiness and find more occasion for laughter than most people with the so-called blessings of civilization.

YOUTH AND THE FUTURE: General Report.

By the American Youth Commission. American Council on Education, Washington, D. C. \$2.50. xix + 296; 1942.

This is a report based on a survey of the conditions that affect the 22 million youth between 16 and 24 in the United States. Six years were spent by the committee in collecting and analyzing the data concerning all problems relating to the care and education of the nation's youth. The Introduction to *Youth and the Future* was written by Owen D. Young. In the preparation of the report "the major objective has been a philosophy which would be applicable both in war and in peace." We quote briefly some of their main findings:

The schools, forming the largest public agency for the training of youth, must revise many of their programs and undertake new ones. The promotion of literacy must continue to be principal among their functions.

Before such a level [a level where all children and youth, regardless of race, will receive at least a sound elementary school education] can be achieved for all youth in the nation, the Commission believes that the federal government must provide funds for the equalization of educational opportunity between the states since some are rich and some poor in resources.

Much of the present duplication and overlapping of authority and funds could be eliminated by a re-districting of the school service areas; . . .

Provision of a sufficient number of schools for all youth will be unavailing unless the quality of instruction is immeasurably improved.

Financing of schools will not be enough; financing of the costs of education to the individual pupil must be undertaken in many cases, the Commission finds, as it states that all youth should be *enabled* to attend school up to the age of 16.

. . . during the immediate emergency period the Commission believes that rehabilitation camps should be established for youth turned down by the selection agents for the Army. It also proposes that a thorough physical examination be made available, free of charge, to every young American, immediately after his or her eighteenth birthday, . . .

In the future, health programs must also be instituted considerably before this "youth health year."

Because of the mounting number of youthful crimes [as many as one third of all persons arrested for offenses are under 25] the Commission believes with the American Law Institute that Youth Correction Authorities should be created in all states which will separate the youthful offenders from the older criminals during trials and while sentences are being served.

The Commission recommends creation of a public work youth agency within the Federal Security Agency where personnel can be in constant contact with the other social agencies whose programs impinge on the welfare of youth.

. . . by teaching youth how to use their leisure time wisely much of the mental illness which was found to be an accompaniment of unemployment can be eliminated.

**PRACTICAL FINGERPRINTING.**

By B. C. Bridges. With a Foreword by August Voll-

mer. Funk and Wagnalls Company, New York and London. \$4.00. 7½ x 5½; ix + 374; 1942.

Finger prints are an unforgeable signature, already established as indisputable legal evidence and a definite means of identification. The most complete up-to-date material on the subject is published in this practical handbook.

Beginning with a concise outline of the history and biological significance of fingerprints, the author leads to the procedure for taking fingerprints, ridge counting, tracing and filing, etc. A detailed account of new methods of uncovering latent fingerprints and their application in criminal investigation is an outstanding feature of the book. Careful inspection and tests decide the method and materials to be used in retouching a fingerprint. Forty-eight different powder materials and twelve powder formulas are listed with instructions for their use in the "powdering fingerprint method". A photograph of the fingerprint prior to and at several stages in its development is first recommended. The method of "lifting latent fingerprints" offers advantages when prints are found in places where they cannot be photographed successfully. This technique and the materials necessary are explained fully. Another "fuming process method" plus "ink", "heat" and "casting" methods covers the subject of latent fingerprints with the latest facility of modern science. A full explanation is given of the Vucetich and the Henry systems of filing and classification, both of which serve as a basis for most other methods.

The work is authoritative being written by a specialist who served a number of years as instructor in this branch of science. It should be useful for police personnel, civic and state officials, students in police recruit training schools, and in colleges having law enforcement courses.

**IN ALASKAN WATERS.**

By Alfred Wolfe. The Caxton Printers, Caldwell, Idaho. \$3.00. 9 x 6; 196; 1942.

In this very interesting book Mr. Wolfe, a fisherman of long experience, gives us in simple direct words a clear account of his numerous trips fishing for deep sea salmon and halibut off Cape Flattery and British Columbia in the summer, and as far north as southeastern Alaska in the winter. The various methods of deep sea fishing are explained and illustrated with accuracy and detail. Up until 1914, the old style type of dory fishing was used entirely. About this time a new method came into use, the "long line system" in which the setting and the hauling of the gear and nets was done directly from the vessel—one of the chief advantages being that men could fish with much less hard labor and in much worse weather than possible when dories were used.

The trips described lasted from two weeks to two months with a catch varying from a few pounds to a

lucky twelve hundred thousand with a good profit shared equally.

One small but interesting incident centers around the catching of a rare "left-handed" halibut with gills and all organs located on the left side instead of on the right as normally. Only three of this type were ever seen in his long experience.

The author discusses at length the "worst marine disaster in the history of the Pacific coast"—the sinking of the Princess Sophia near the end of World War I with a 100 percent loss of life.

From reading this book one cannot help but be impressed with the courage, fortitude, resourcefulness, and endurance exhibited by these fishermen who make their living in these dangerous waters.



THE CLARKS. *An American Phenomenon.*

By William D. Mangam. With an Introduction by Edward Alsworth Ross. Silver Bow Press, New York. \$2.50. 8 x 5½; ix + [257]; 1941.

If the unsuspecting reader should feel that it is impossible that the limits of a single family should embrace such a high concentration of immorality as the author attributes to the Clarks, let him recall that the latter were endowed with sufficient wealth to prosecute a libel suit, had there been the least doubt as to the accuracy of the author's statements.

Perhaps the most striking disclosure made in the entire book is that one of the Clarks kept a mistress, not for the purpose which mistresses ordinarily serve, but as a red herring to draw across the trail in case the police became too inquisitive about the practices indulged in behind his closed doors. He considered the reputation he was able to enjoy as the result less malodorous than the one he would have acquired if the facts on his way of living became public property.

Reviews of pornographic literature are not new to these columns, but all previous examples pale into innocuous innocence when viewed in the light of the lurid hues of this masterpiece. One wonders why the author did not employ his talents in a worthier task.

To the Clark family is hereby unanimously awarded the gold-plated gas mask.



NEEDLE TO THE NORTH: *The Story of an Expedition to Ungava and the Belcher Islands.*

By Arthur C. Twomey, in collaboration with Nigel Herrick. Houghton Mifflin Company, Boston. \$3.50. 9 x 6; viii + 360; 1942.

Needle to the North is a vivid account of a scientific expedition to Ungava and the Belcher Islands, located in the sub-arctic region of the Hudson Bay and the northern half of the Labrador Peninsula. These desolate regions,

unheard of by the general reader, have long lain unchanged and uncharted.

The book, divided into two sections, first tells of Ungava and describes the quest of the mysterious unknown inland sea "Kasogea", which is almost a legend. Twomey, an ornithologist, and Douth, mammalogist, both of the Carnegie Museum, experienced considerable adventure, difficulties and human drama before their purpose was successfully accomplished. The scientific report on Kasogea has not yet been published.

The second section of the book is concerned with the Belcher Islands, and their strange and primitive peoples. Civilization came late to the Belcher Island Eskimo, yet his very sensitive mind and adaptability to new ways, makes him already a doubtful example of a natural igloo-man. "Before you would dare assume that he has learned to use it, the hunter of the Belchers will make your mechanical gadget an integral part of his life". The author describes, among his experiences in the Belcher Islands, the quick change from the long winter to the short spring and summer with its numerous flowers, buds, insects, etc., which come to life for this brief season.



FAMILY EXPENDITURES FOR CLOTHING: *Five Regions.* U. S. Department of Agriculture Miscellaneous Publication No. 422. Consumer Purchases Study. Urban and Village Series.

By Maryland Y. Pennell, Day Monroe, Kathryn Cronister, Geraldine S. DePuy, and Marjorie W. Ellsworth. Government Printing Office, Washington, D. C. 35 cents. 9½ x 5½; iii + 329; 1941.

CHANGES IN ASSETS AND LIABILITIES OF FAMILIES: *Five Regions.* U. S. Department of Agriculture Miscellaneous Publication No. 464. Consumer Purchases Study. Urban, Village, and Farm Series.

By Dorothy S. Brady, Day Monroe, Janet Murray, Yetta A. Carmel, and Marjorie Ellsworth. Government Printing Office, Washington, D. C. 25 cents. 9½ x 5½; v + 226; 1941.

FAMILY EXPENDITURES FOR HOUSING AND HOUSEHOLD OPERATION: *Five Regions.* U. S. Department of Agriculture Miscellaneous Publication No. 457. Consumer Purchases Study. Farm Series.

By Hazel Kyrk, Day Monroe, Dorothy S. Brady, Collette Rosenstiel, and Edith Dyer Rainboth. Government Printing Office, Washington, D. C. 25 cents. 9½ x 5½; v + 201; 1941.

In all three of these reports the first part deals with a discussion of the scope and organization of the study and the general summary of the findings, with the data collected exhibited in detail in tables in the latter part. In each case a wealth of material has been collected and has been so arranged that future workers along these lines will find the present study of great usefulness.

ZOOLOGY

ANIMALS ARE MY HOBBY.

By Gertrude Davies Lintz. Robert M. McBride and Company, New York. \$2.75. 8 x 5½; 301; 1942.

This is the entertaining and at times instructive autobiography of an unusual woman who admits frankly that "rare animals—from difficult to impossible ones—have been the irresistible lure of my life. Just as some women are most attracted by problem children, I am attracted by problem animals." In her New York home Mrs. Lintz has brought up sixteen great apes, including the now much advertized gorilla "Gargantua", over two hundred St. Bernard dogs, and a random assortment of other animals. The largest and most interesting part of the book deals with the lives of the anthropoid apes who enjoyed amazing freedom and devoted care in the writer's extraordinary household, where they thrived in spite of many an initial illness. Mrs. Lintz's remarkable success in raising her many simian *prima donnas* was due chiefly to her full appreciation of the need of these apes for companionship, entertainment, and exercise, factors which are all too frequently ignored in zoological gardens. For the author's great devotion nothing appears to have been too much; with a sick baby mountain gorilla she patiently tried to "pinch-hit for a mother gorilla" by chewing food into a soft pap until her jaws ached and then transferring it to the gorilla's mouth. Incidentally, this ape was regarded by Mrs. Lintz as "the most feminine creature in the house," but was really a male who grew to huge size. Eventually he had to be sold to a Zoo, though not until sometime after he had severely mauled his benefactor. Like nearly all apes, Gargantua also became untrustworthy with advancing age and had to be confined in a welded steel cage in the Lintz sun parlor. He had passed the 400-pound mark when one night he escaped and made a bee-line for the author's bedroom. That she got him back safely is a miracle and the account of it is very worth reading.

The author summarizes her unique experiences by maintaining that the gorilla always wants to keep the peace and that if he is not "a man on his way up, to me he seems a brother." Quite evidently she thinks more highly of all her apes than of some human beings—no wonder, since two of her apes were poisoned and one had acid thrown over him and later was given acid to drink by mean human morons.

Some of the illustrations are excellent and many of the chapters contain accurate descriptions of the psychological nature of the two great African apes.



ORNITHOLOGISTS OF THE UNITED STATES ARMY MEDICAL CORPS. *Thirty-six Biographies.*

By Edgar Erskine Hume. With a Foreword by Alexander Wetmore. The Johns Hopkins Press, Baltimore. \$5.00. 10½ x 7½; xxv + 583; 1942.

It was under the guidance and encouragement of Spencer Fullerton Baird, Assistant Secretary of the Smithsonian Institution from 1850 to 1878 that many young surgeons of the Army Medical Corps developed an interest in birds. Baird assisted many of these by suggesting details and assignments for expeditions during the period of the opening up of the West. The names and contributions to systematic ornithology of Coues, Bendire, Cooper, Heermann and Mearns are familiar to most ornithologists of the present generation. It is also a rather well-known fact that the army stations and travels of these men in the West gave them the opportunities of pioneers in the study of birds. That we can add to the contributions of these great men those of many others from the same branch of the military service is, however, probably somewhat surprising to most students of bird life.

Colonel Hume has collected in the present volume a great store of information about the thirty-six men of whom he writes. He has obtained much valuable and interesting data from the archives of the Army Medical Corps which give us information not heretofore publicly known. The biographic sketches are interestingly written and briefly summarize the activities of these men, both from the point of view of their army duties and their ornithological interests. In many cases extracts of their writings are given. These include very interesting descriptions of explorations both in this country and abroad. Each biography contains one or more illustrations of the subject, and there are many historically interesting photographs and sketches of old army posts.

Indeed we have in this volume a kind of "personal bibliography" of the development of ornithology in this country during the nineteenth and early part of the twentieth century. In the words of the author, "It is hoped that these bibliographies of medical officers of the United States Army who have contributed to ornithology will establish one more record of achievement for the Medical Department in a highly specialized field of science." The book is of unusual value both to the medical historian and to the student of bird life.



LIFE HISTORIES OF NORTH AMERICAN FLYCATCHERS, LARKS, SWALLOWS, AND THEIR ALLIES. *Order Passeriformes. United States National Museum Bulletin 179.*

By Arthur Cleveland Bent. Smithsonian Institution, Washington, D. C. \$1.00. 9½ x 6; xi + 555 + 70 plates. 1942 (paper).

This is the fourteenth in a series of bulletins of the United States National Museum on the life histories of North American birds. The general plan and method of presentation of the data are the same as that followed in previous bulletins, and the same sources of information have been utilized. The nomenclature of the 1931

check-list of the American Ornithologists' Union has been followed.

Life histories of the best-known subspecies of each species are given as completely as possible. To avoid duplication in describing the others only the characters of the subspecies, its range, and any life habits peculiar to it are included. In many cases certain habits which are probably common to the species as a whole have been recorded for only one subspecies. These are described for the species on which the observations have been made. The distribution of the species as a whole is given, with only rough outlines of the ranges of the subspecies, which in many cases cannot be accurately defined.

The data on each species are usually arranged under the following headings: Courtship, Nesting habits, Eggs, Plumages, Food, Voice, Field marks, Distribution (including spring and fall migration dates). The plumages are described in only enough detail to enable the reader to trace the sequence of molts and plumages from birth to maturity and to recognize the birds in the different stages and at the different seasons.

In addition to the excellent treatment of the life histories and habits of these interesting American birds there are seventy plates of collected photographs. These are of the usual high quality found in this series of bulletins. Many of the birds, their nesting habitats and nests are illustrated. No small part of the value of this bulletin lies in its plates.



CATALOG OF THE TYPE SPECIMENS OF MAMMALS IN THE UNITED STATES NATIONAL MUSEUM, INCLUDING THE BIOLOGICAL SURVEYS COLLECTION. *Smithsonian Institution, United States National Museum Bulletin 178.*

By Arthur J. Poole and Viola S. Schantz. Government Printing Office, Washington, D. C. \$1.25. 9½ x 6½; xiii + 704; 1942 (paper).

In 1901 the first type list of mammals in the United States National Museum was published (*U. S. Nat. Bull.* 62, 325). The present volume, the second such catalog to be issued, includes also those specimens now in the collection made by the Fish and Wildlife Service (the two collections are kept separate but are in adjoining laboratories). A total of 2,824 type specimens are listed of which 1,409 are new additions since the publication of the first type list. Large series of specimens have been used in the work, and nearly every prominent mammalogist, so the authors say, is represented—Audubon, Allen (J. A.), Baird, Cope, LeConte, and others of the earlier period; Bailey, Howell (A. H.), Lyon, Merriam (C. H.), Miller, and many others of more recent times. While numerous expeditions have contributed to the collection, the type specimens of the Malayan and African mammals have come from two main sources, namely the Malayan explorations of the late Dr. W. L. Abbott (1897–1909) and the Smithson-

ian and Rainey African expeditions (1909–1910, 1911–1912). The older type specimens of North American mammals have also come from two main sources, those collected about the middle of the nineteenth century by governmental exploring parties and those recently collected by the Biological Survey.

The material is well arranged and the catalog will be of great usefulness to those who have occasion to consult it. At a glance all the necessary information about any desired form is available: place and date of original description, U. S. Nat. Mus. catalog number, nature of specimen (whether there is present skin, skull or other parts of skeleton; how preserved, etc.), age and sex, locality, date of collecting, name of collector, original number of specimen, date when cataloged, and condition of specimen at present time.



REPRESENTATIVE NORTH AMERICAN FRESH-WATER FISHES.

By John T. Nichols. Illustrated by Andrew R. Janson. *The Macmillan Company, New York.* \$1.25. 6¼ x 4; 128; 1942 (paper).

This little vest-pocket book is designed to aid the angler, or anyone else interested, in the identification of the common types of North American fresh-water fishes and to afford him some information concerning their habits and habitats, their adaptations and their evolutionary relationships. The book consists of sixty full-page illustrations, half of them in color, of representative fishes, with a single page of text accompanying each figure. The illustrations are uniformly excellent and the amateur should find it easy to make an approximate identification of any specimen which comes to hand, simply by comparison with the figures. This being the case, there has been no attempt to provide a key or to give a detailed description of taxonomic characters. Instead the text is mainly devoted to accounts of interesting habits or adaptations of the fish under consideration or to general ichthyological problems which it suggests. Thus the discussion of the paddlefish (*Polyodon*) provides an opportunity for some account of relict species; the evolution of the swim-bladder into a respiratory apparatus is considered in connection with the bowfin (*Amia*) and the migrations of anadromous and catadromous fishes are discussed in the sections on the shad and the eel. In this way Nichols has been able, in a very short space, to give information on such a wide variety of subjects as breeding habits, nest building, concealing coloration, the inheritance of albinism and the evolution of the cave-fishes. The text is written in a simple straightforward style with no attempt to "talk down" to the layman.

This reviewer feels that the book fulfils most admirably the double function which such a brief introductory work should have. It provides a clear and useful means for ready identification of specimens while at the same

time effectively stimulating interest in the broader aspects of ichthyological science.



THE RAT in Laboratory Investigation.

Edited by John Q. Griffith, Jr. and Edmond J. Farris.
By a Staff of Thirty Contributors. J. B. Lippincott
Company, Philadelphia and London. \$7.50. 9 x 6;
xiv + 488; 1942.

The albino rat is the most widely used laboratory animal today. It has been found to be an ideal animal for research in many disciplines of experimental biology. A volume, such as this one, which emphasizes techniques and procedures, has been needed for a long time. It is thus destined at the outset to serve a useful purpose.

Some of the numerous and varied subjects treated by the different authors are: breeding, gross anatomy, embryology, diet, teeth, digestive system, metabolism, central nervous system, psychology, circulatory system, bio-assay, hematology, histology, surgery and parasitology. The chapters on gross anatomy, dietary requirements, teeth, and surgery are particularly complete. In almost all chapters experimental methods and techniques receive the major emphasis. The illustrations are numerous and well selected. A useful bibliography is provided at the end of each chapter. The index is adequate.

Naturally many of the methods applied to, and conclusions derived from, work on rats, while having particular reference to investigations on the rat, are applicable to experimental work in general. The book should be useful, therefore, not only to investigators who work with rats but also to general mammalian physiologists, histologists, etc.

In many institutions the rat is as familiar to the teacher as to the investigator. Those who teach experimental subjects in the biology curriculum will, therefore, find this volume an excellent reference work. The book is one which is to be highly recommended to investigator, teacher and student alike.



THE LIFE OF LANGSTROTH.

By Florence Naile. Edited, with a Foreword and an Introduction by Everett Franklin Phillips. Cornell University Press, Ithaca. \$2.50. 8½ x 5½; 215; 1942.

Lorenzo Lorraine Langstroth, the "Father of American Beekeeping," was born in Philadelphia in 1810 and died in 1895. He was educated at Yale and ordained to the Christian ministry, which he practiced for several years until ill-health unfitted him for a regular charge. He then took up beekeeping which had already interested him as a hobby. His studious observations of the habits of bees led to his invention of the removable-frame hive and the publication, in 1853, of *The Hive and*

the Honey Bee, the first American handbook for beekeepers. He also was a prolific contributor of articles to the *American Bee Journal* and *Gleanings in Bee Culture* from the time of their foundation in 1861 and 1874, respectively. And he took part in the long-continued, but eventually successful, attempts to import Italian bees and to naturalize them in this country. This is the outline, in brief, of Langstroth's life and work and, until the publication of this book, represents about all (or more) that was generally known about him. Miss Naile is his first biographer. There is evidence of painstaking study of source material for collecting and putting in order the less known facts of Langstroth's life, but the book is not dull. In fact, it should be of interest even to those who have no intimate knowledge of beekeeping.



THE COMMERCIAL FISH CATCH OF CALIFORNIA FOR THE YEAR 1940. *State of California, Department of Natural Resources, Division of Fish and Game, Fish Bulletin No. 58.*

By the Staff of the Bureau of Marine Fisheries. California State Printing Office, Sacramento. 9 x 6; 47; 1942 (paper).

This is the seventh of a series of "Catch Bulletins." These are issued for the purpose of making available the summaries of commercial fish landings in each region of the State of California. Aside from the data on pounds of fish landed (these are given separately for each kind of fish) the reports are of considerable interest from several points of view. Data are included concerning numbers and nativity of commercial fishermen and number of boats of each type engaged in the fishery; the shifting from one type of fishing to another (a notable example of this is the rapid development of the shark fishery because of the high price offered for the liver oils); the development of sport fishing with its requirement of small fish for bait—chiefly sardines and anchovies. In 1940, 2389 tons of live bait were used for this purpose.

The total pounds of fish landings for 1940 came to 1,296,048,348; for 1939 the catch was very nearly 200 million pounds greater. This large withdrawal of fish from California waters each year must have, over a period of years, a profound effect on the fish population of the region.



THE INTERNATIONAL PROTECTION OF WILD LIFE: *An Examination of Treaties and Other Agreements for the Preservation of Birds and Mammals.*

By Sherman Strong Hayden. Columbia University Press, New York. \$3.00. 8½ x 5½; 246; 1942.

When an animal maintains a seasonal migration across several sovereign states it can be conserved only by

international treaty. At a time like this when there is so much international dissension and where national policies conform to present wants rather than to future needs, it seems impossible that any sort of agreement for the preservation of wild life could be reached. It is true that the outlook for seals, whales, and migratory birds looks black, but it is by no means hopeless.

In this work is told the story of what has been done in the past, both by reciprocal agreement and through the League of Nations, and the average reader is likely to be surprised by the advances that had been made prior to the beginning of the present war. But it must be remembered that that was only a beginning, and that when sanity returns to a warring world it will be necessary to have some more international agreements.

The book is amply documented and well worthy of serious study.



PRAIRIE DOG TOWN.

By Margaret Thomsen Raymond and Carl O. Mohr. Dodd, Mead and Company, New York. \$1.50. 8½ x 6½; 56; 1942.

The life story of Mr. Prairie Dog is here recounted for the youthful reader. His day to day activities are followed from his infancy to the time when he assumed the onerous responsibilities of a family head. The industry and ingenuity with which he builds his burrow and his constant wariness in avoiding his enemies are absorbing topics and one soon comes to respect Mr. Prairie Dog as an independent and self-reliant little chap who, even in times of greatest hardship and danger, is filled with the joy of living. The book is illustrated by an excellent series of photographs of prairie dogs and their neighbors, the burrowing owl, the prong-horn antelope, the jack-rabbit and others. The prairie dog's enemies are also portrayed; the hawk, the ferret, the coyote, the badger and the rattlesnake. In addition there is a series of lively sketches of some of the activities of these animals. This is a fine example of the best type of nature book for children.



HORNS AND ANTLERS.

By Wilfrid S. Bronson. Harcourt, Brace and Company, New York. \$2.00. 8½ x 6; 143; 1942.

The natural history of the North American deer and antelopes is here set forth in the same engaging style which distinguishes Mr. Bronson's book on the rodents. Sympathetic interest and painstaking, accurate observation have combined to produce a lively and authoritative picture of the habits of the various native ruminants of this continent and to bring out the differences between them. Separate chapters are devoted to consideration of the whitetails, the mule deer, the wapiti, the moose, the reindeer and caribou, the prongbucks

and the mountain "goats." The author's well-known paintings of natural history of subjects are represented by four full-color plates and 46 black and white illustrations.

This is a work which will prove of special interest to the student of natural history and to the hunter. Moreover, because of the large amount of first-hand information about the habits of the deer family which it contains, it will be a useful reference book for the professional zoologist.



NOTES ON A COLLECTION OF FISHES FROM ANTIGUA AND BARBADOS, BRITISH WEST INDIES.

By Albert W. C. T. Herre. Stanford University Press, Stanford University, California; Oxford University, London. \$1.25. 9½ x 6½; 21; 1942.

The identification and description of some 90 species of fish representing 68 genera and 41 families, collected by Dr. Walter K. Fisher in 1918 from the waters around Barbados and Antigua, is successfully undertaken in this report. The difficulties inherent in measuring and describing the colors of various specimens of fish which have been preserved for nearly 25 years are indicative of the laborious and painstaking observations essential to a study of this sort.

In addition to the listing of measurements, colors and sites of collection for each species, the author includes pertinent discussions on the minor distinctions between various forms, the errors in earlier taxonomic works, and the value of further studies of the fish from this region.

The work carries a short table of contents, but no index.



ZOOLOGICA. Scientific Contributions of the New York Zoological Society. Vol. XXVII, Part I, Numbers 1-8.

New York Zoological Society, Zoological Park, New York. 75 cents. 10½ x 7; 48 + 5 plates + 1 folding map; 1942 (paper).

This number contains the following papers:

Social and respiratory behavior of large tarpon, by C. M. Breder, Jr. (1 text figure); Tetanus in an elephant (*Elephas maximus*), by Leonard J. Goss; Descriptive ecology of La Cueva Chica, with especial reference to the blind fish, *Anoptichthys*, by C. M. Breder, Jr. (1 text figure and 3 plates); Quantitative serologic relationships within the Artiodactyla, by Joseph G. Baier, Jr. and Harold R. Wolfe (1 text figure); Observations on the electric discharge of *Torpedo occidentalis*, by C. W. Coates and R. T. Cox, (4 text figures); The Ampulicidae and Sphecidae (Sphecinae) taken at Kartabo and other localities in British Guiana. (Hymenoptera), by H. T. Fernald; A Résumé of Mexican Snakes of the Genus *Tantilla*, by Hobart M. Smith; Eastern Pacific expeditions of the New York Zoological Society. XXX. At-

lantic and Pacific fishes of the genus *Dixonina*, by William Beebe (2 plates).



THE ANIMAL BOOK: American Mammals North of Mexico.

By Dorothy Childs Hogner and Nils Hogner. Oxford University Press, New York and London. \$3.50. 10½ x 8; 223; 1942.

This is a handbook of mammals living on the North American continent and in adjacent waters north of Mexico. The habits, appearance, and range of about one hundred and seventy mammals, both familiar and unfamiliar, are described in a simple, direct, accurate manner for juvenile readers. The material was compiled from first-hand study of the animals, much of it during "travel with a tent and camp kit over many sections of the continent."

The illustrations, more than one hundred pen-and-ink sketches in black-and-white, by the author's artist husband are an essential part of the work. This book should be useful in schools, camps, libraries, or any place where accurate accounts and pictures of North American mammals are needed for young folks.



THE TALE OF THE PROMETHEA MOTH.

By Henry B. Kane. Alfred A. Knopf, New York. \$1.25. 9 x 7; 24 unnumbered pages + 22 plates; 1942.

This beautiful little book is the third volume in the "Wild World Tales" series by Kane in which once more he combines facts, beautiful photographs and attractive pen-and-ink sketches to give his readers a true and exciting story of nature.

The Promethea is one of the largest, handsomest and most common of the great moths, and unlike many of them, flies in the late afternoon at dusk. The account of its interesting life-cycle is given so simply and beautifully that it will interest mature as well as young readers. The twenty-three full-page photographic illustrations accompanying the text are particularly fine in both composition and detail and alone are well worth the price of the book.



WONDERS OF THE SEA.

By Gladys Pratt Freund. Illustrated by Rudolf Freund. Random House, New York. \$1.00. 11 x 9; 36; 1942.

This very colorful book is designed primarily for introducing to juvenile readers a few of the more spectacular of the animals and plant-like animals that live in the ocean.

Some of the "wonders" selected by the author for

description and illustration are: sponges, corals, sea anemones, giant clams, cephalopods, barnacles, jelly fish, various "queer fish" such as puffers, flying fish, angler fish, deep sea luminous fish, and the giant whales, porpoises and dolphins. The book contains a good deal of basic information and is interesting to read.

More than a dozen full-page, highly-colored decorative drawings by Rudolf Freund illustrate the text.



AMERICAN BUTTERFLIES AND MOTHS.

By Cecile Hulse Matschot. Illustrated by Rudolf Freund. Random House, New York. \$1.00. 11 x 8½; 70; 1942.

In this artistic, tastefully arranged and practical book, the author has given us the complete life-story of seventy-three of our most common butterflies and moths. The detailed descriptions aided by reference to numbers of full-color plates and black-and-white sketches by Rudolf Freund enable one to identify with ease the butterflies and moths seen in gardens, parks, and on walks in the fields and woods. The author has had considerable experience as a naturalist both in Latin America and in this country. The book is not intended for specialists but rather to introduce these most fascinating of all insects to us.



BRITISH BIRDS on Lake, River and Stream.

By Phyllis Barclay-Smith. With sixteen colour plates after the originals in *The Birds of Great Britain* by John Gould. Penguin Books, Ltd. Harmondsworth, England. 25 cents. 7½ x 5½; 31 + 16 plates; 1941.

This popular little book contains sixteen color plates reproduced from the originals in *The Birds of Great Britain* by John Gould. The colors and composition of the plates are good. In addition to the plates the book has a brief biographic sketch of the life of John Gould, the well-known British and Australian ornithologist. There are also very brief but interestingly written descriptions of the life habits of the sixteen bird species. Only the most common fresh-water birds are described.



TRANSACTIONS OF THE SAN DIEGO SOCIETY OF NATURAL HISTORY. Volume 9, Nos. 32 and 33. A Vertebrate Faunal Survey of the Organ Pipe Cactus National Monument, Arizona, by Laurence M. Huey; Notes on Some Mexican and Californian Birds, with Descriptions of Six Undescribed Races, by A. J. van Rossem.

Society of Natural History, San Diego, Calif. 10½ x 6½; No. 32, 21; No. 33, 8; 1942 (paper).

OFFICIAL ILLUSTRATED GUIDE BOOK TO THE PHILADELPHIA ZOOLOGICAL GARDEN.

By Roger Conant. *Zoological Society of Philadelphia*. 25 cents. 8½ x 5½; 107; 1941.



BOTANY

HOME VEGETABLE GARDENING.

By Charles H. Nissley. With an Introduction by William H. Martin. Illustrated by Ruth Nissley. *Rutgers University Press, New Brunswick, N. J.* \$1.50. 7½ x 5; x + 246; 1942.

25 VEGETABLES ANYONE CAN GROW.

By Ann Roe Robbins. Illustrated by Leonard J. Robbins. *Thomas Y. Crowell Company, New York.* \$2.25. 9½ x 6; xii + 219; 1942.

THE FOOD GARDEN.

By Edna Blair. Illustrated by Laurence Blair. *The Macmillan Company, New York.* \$2.00. 10 x 9½; 148; 1942.

All three of these books belong in the "how-to-do-it" category and were written for those persons whose first venture at vegetable growing is the Victory garden. *Home Vegetable Gardening* is the most comprehensive of the three. In addition to the specific instructions for growing each of more than 60 vegetables and herbs, it contains preliminary chapters on gardening equipment, the selection of seed, preparing and improving the soil, growing early plants for transplanting, storing vegetables for winter use, and garden pests and their control. A supplementary chapter gives instructions for saving and treating seed.

Mrs. Robbins' book contains brief, but adequate, information on the history, food values, culture, and habits of growth, storing, canning, and recipes for cooking each of the 25 vegetables as well as giving directions for their planting and cultivation. It is provided with a washable cover and may be used and consulted out in the garden.

The third book is the most profusely illustrated. The directions given for the growing of most of the 49 vegetable and salad plants, 16 herbs and 17 fruits and berries selected by the Blair's for discussion, are accompanied by series of drawings depicting various steps in their cultivation.



PROPAGATION OF PLANTS. *A Complete Guide for Professional and Amateur Growers of Plants by Seeds, Layers, Grafting and Budding, with Chapters on Nursery and Greenhouse Management. Revised and Enlarged Edition.*

By M. G. Kains and L. M. McQuesten. *Orange Judd Publishing Company, New York.* \$3.50. 9 x 6; xi + 639; 1942.

As the original edition of this standard reference book was published 22 years ago and is now both out of date and out of print, this revision fills a definite need. It has been considerably enlarged and changes and corrections have been made throughout to conform with the most recent data available from a review of the world literature in this field. "The text has been so arranged that the propagator... can get a clear exposition of whatever subject interests him, without being annoyed by pedagogical material... the teacher, the experimenter, and the student will find abundant reference to text and illustrations in the 50 practicums placed toward the close of the book." In addition to the detailed discussions of methods of aiding germination, seed testing, various kinds of propagation, pest control and so forth, there are plant lists and condensed rules for propagation of special value when unfamiliar plant material is being dealt with, and a list of Federal and State regulations and quarantines. The addition of new illustrations brings the total to 350 plates, many of which contain two or more pictures. Unfortunately, not all of these are clear enough to enable the easy perception of details. References to tables, illustrations and the institutions and authors whose work has been cited in the text are listed in the same index as the subjects and plant varieties discussed.



A TEXTBOOK OF BACTERIOLOGY. *Third Edition, Revised.*

By Thurman B. Rice. *W. B. Saunders Company, Philadelphia and London.* \$5.00. 9½ x 5½; xii + 560; 1942.

The stated purpose of this text (cf. Q. R. B., V. 11, p. 104 and V. 14, p. 90 for notice of earlier editions) is to serve as a practical aid to the general practitioner or student who might wish a full understanding of the subject, but who cannot find time to go into all the five theoretical points. It is a practical rather than a theoretical text. By a thorough sifting of material, the author has obtained a very condensed treatment. Morphological and cultural characteristics are held to real essentials. The emphasis is rather on disease characteristics with efficient diagnosis, prognosis treatment and general management as the end.

Although the present edition has been brought up to date to some extent, there are no extensive changes in the text material. Slight additions have been made in some chapters as, for example, in those of rickettsia, filterable viruses, etc. Information on "special bacteriology," collection of samples, etc., is appended. There is a useful index, but unfortunately no bibliography, a regrettable omission in view of the condensed nature of the text.

This book should be of great use both for beginners, as an introduction, and for more advanced students and practitioners, as a practical review book.

SOYBEANS: *Gold from the Soil.*

By Edward Jerome Dies. *The Macmillan Company, New York.* \$1.75. 8 x 5½; 112; 1942.

Although soy bean culture in China was ancient when Abraham resided in Ur of the Chaldees its introduction to the western world is of such recent date that a brief volume is adequate to cover its history and to recount some of the purposes to which it is adapted.

The importance of the soy bean as a foodstuff is due to its high proteid and vitamin B content, and its low starch content. Agriculturally it is of importance because it requires less care between planting and harvesting than most crops, and its industrial significance may be judged from the fact that one automobile manufacturer is seriously considering it as a source of plastic from which bodies may be constructed.

Although only one species of soy bean is known, 126 varieties have been introduced into the United States, which differ in their proportions of oil, starch, number of beans to the pound, age at maturity, etc. Several pages of comparative statistics are given, but owing to the lack of probable errors it is impossible to tell whether the varieties are really distinct or not.

The book is well provided with graphs illustrative of the fluctuations in value and size of crops from year to year, and a bibliography of over 200 items adds to its usefulness.

**TEXTBOOK OF DENDROLOGY: *Covering the Important Forest Trees of the United States and Canada. Second Edition.***

By William M. Harlow and Ellwood S. Harrar. *McGraw-Hill Book Company, New York.* \$4.50. 8½ x 6; xv + 542; 1941.

The major changes that have been made for this edition are the inclusion of range maps for all the species set in text type and tables of "distinguishing characteristics" for groups of these species. The nomenclature in the first edition followed the American Code. In consideration of the recent adoption of the International Code by the United States Forest Service, appropriate changes and additions have been made in the nomenclature used in the present edition. As the book is designed for use in a beginning course in forestry only, the species of greatest importance to forestry, commerce and industry in this country are treated. Numerous excellent photographs and drawings clarify the text. The authors have provided a glossary, a list of bibliographical references, selected for their significance or recency, and an index which indicates also the pages where half-tone illustrations of the item in question occur.

ITINÉRAIRES BOTANQUES DANS L'ÎLE DE CUBA: (*Première Série*). *Contributions de l'Institut Botanique de l'Université de Montréal, No. 41.*

By Frère Marie-Victorin and Frère Leon. *Institut Botanique de l'Université Montréal, Montréal.* \$2.50. 9 x 6; 496 + folding map; 1942 (paper).

As part of its active program of research work, The Botanical Institute of the University of Montreal organizes expeditions to various locations in the western hemisphere for the purpose of identifying, collecting and studying the native flora of the region. The present monograph, number 41 in The Institute's series of publications, is a report of just such an expedition to Cuba in 1939. The geographical, physiographical and geological features of the island are considered in relation to the ability of various types of terrain to support plant life. Then, in log form, the work presents the chronological activities of the expedition as it covered its extensive itinerary. Particular note is made of the taxonomic, physiological, ecological, and pathological characteristics of the flora of a considerable portion of the island.

The work is profusely illustrated with photographs, charts and maps showing the distribution of the various species of plants. A large gatefold, cross-key map of Cuba, for ease in locating points of interest in the expedition, and an index of scientific names are appended.

**SCIENCE IN THE GARDEN.**

By H. Britton Logan and Jean-Marie Putnam, in consultation with Lloyd C. Cosper. Foreword by Dr. F. W. Went. *Duell, Sloan and Pearce, New York.* \$2.50. 9½ x 5½; xiv + 255; 1942.

The first three chapters of this book sketch briefly some of the major discoveries from early times to the present that have aided in the development of scientific gardening. The other chapters are more specific with respect to the various phases and chores in the propagation of plants, such as pollinization and the evolution of new plants, chemical acceleration of seed germination, pruning, the effects of light, vitamin B₁, colchicine and other substances on plant growth, and the like. In pointing out the scientific basis for many of the chores of the gardener, the authors explain, wherever possible, the "why" as well as the "how" of the procedure in question. Numerous experiments that may be carried out with little equipment and small space are suggested and outlined in the last chapter. Written for the layman who is interested in "dirt gardening," the book is authoritative and it is hoped will inspire new contributions to the science of plant propagation.

CHEMICAL GARDENING. *Latest Developments in Soiless Culture of Plants.*

By D. R. Mallin. Chemical Publishing Company, Brooklyn. \$2.25. 8½ x 5½; vi + 159; 1942.

Chemical Gardening is a new 150-page manual for the popular occupation of growing plants in liquid and sand cultures. This book compares very favorably with earlier publications on soiless gardening in that it is mainly factual, less extravagant in claims and less superficial in its treatment of basic principles of plant culture than most publications on this subject. A great deal of practical general information on techniques of preparing and caring for soiless plant cultures is concisely presented in 13 separate chapters.

Several nutrient formulae, charts of mineral deficiency and toxicity symptoms, brief treatments of the function of elements and the use of insecticides, etc. are included. The types of equipment and procedures suited for commercial protection and home use are presented separately. The book therefore may be of considerable value to home gardeners in general.

**HISTOIRE DE L'INSTITUT BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL 1920-1940. *Contributions de l'Institut Botanique de l'Université de Montréal*, No. 40.**

By Frère Marie-Victorin. Institut Botanique de l'Université de Montréal, Montréal. \$1.00. 9 x 6; 70; 1941 (paper).

The historical development, scientific activities and publication, personnel, and probable future of The Botanical Institute of the University of Montreal are discussed in detail in this published form of Frère Marie-Victorin's presidential address delivered before the Canadian Society of Natural History, at the Botanical Garden of Montreal, in February, 1940.

The rapid growth of The Institute during the past 20 years, the excellent service it has performed, and the impressive list of publications (this is the 40th) are indicative of a sound foundation and able leadership. We can rightly expect the future contributions of The Institute to be of the same high quality as those of the past. Numerous photographs of the buildings, staff, and classes of The Institute are included in the volume.

**CONE-BEARING TREES OF THE PACIFIC COAST.**

By Nathan A. Bowers. Whittlesey House, McGraw-Hill Book Company, New York and London. \$2.50. 8 x 5½; ix + 169; 1942.

Realizing a real need for something in between the technical treatise and the sketchy "popular" material, the author has prepared this comprehensive yet non-technical field manual for the use of non-botanical tree lovers on mountain trips and in rambling through the forests of the Pacific slope. He offers three keys to

identification—the Needle Key, the Elevation Key and the Geographical Key—with complete directions for their use.

The greater part of the book is taken up with descriptions of the various species conveniently grouped according to geographic districts. There are 57 full-page plates, a glossary and an index.

**PLANT BIOLOGY.**

By Paul Weatherwax. W. B. Saunders Company, Philadelphia and London. \$3.25. 8½ x 5½; vi + 455; 1942.

This book has been designed as a text for a one semester course in botany or for the botany part of a generalized course in biology. Actually, it contains more material than can be covered in a short course, but the material is so arranged that parts, such as the chapters on the great groups of plants, can be omitted or modified to suit the aims of the individual teacher. There is a glossary, with pronunciation indicated, of terms used exclusively in biology or that have some special meaning when used in that field which the student should know—the list is not confined to words used in this text. The book is profusely illustrated with photographs and line drawings, many of them by the author himself.

**PLANT LIFE. *A Textbook of Botany. Second Edition.***

By D. B. Swingle. D. Van Nostrand Co., New York. \$3.00. 9 x 6; xvi + 457; 1942.

The main emphasis in this text is upon the physiology and behavior of plants. It has been prepared for use in a short course in botany, affording students who do not intend to continue the subject further with a good knowledge of the fundamentals and those who do an excellent background for advanced study. The revision consists mainly in the introduction of a little more natural history than the first edition contained, amplification of portions that experience has proved were treated too briefly for clearness, and the addition or substitution of a few new illustrations.

**CONTRIBUTIONS DE L'INSTITUT BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL. No. 37, *Notes sur les Cistes.***

I. *La Collection du Bailey Hortorium*, by Pierre Dansereau. *Introgression des Caracteres de l'Acer saccharophorum K. Kooch et de l'Acer nigrum Michx.*, by Pierre Dansereau and Andre Lafond. No. 38, *Études sur les Hybrides de Cistes.* IV. *Corrélation des caractères du C. salvifolius L.* VI. *Introgression dans la section Ladanium*, by Pierre Dansereau. No. 39, *Studies in the Genus Heterosporium*, by J. Emile Jacques.

Institut Botanique de l'Université de Montréal, Mon-

tréal. 9 x 6. No. 37: 31; 25 cents; No. 38: 67; 25 cents; No. 39: 46 + 6 plates; 50 cents; 1941 (paper).



MORPHOLOGY

THE LYMPHATIC SYSTEM: Its Part in Regulating Composition and Volume of Tissue Fluid. *Lane Medical Lectures. Stanford University Publications, University Series, Medical Sciences, Vol. IV, No. 2.*

By Cecil Drinker. Stanford University Press, Stanford. \$2.25. 10 x 7; 101; 1942.

These outstanding lectures, the 28th series in the group of Lane Medical Lectures, are destined to become classic in their field. Dr. Drinker has summarized in a clear and brilliant manner the present status of knowledge concerning the lymphatics, reviewing the trends of research which have led to the attainment of that knowledge and indicating future lines for productive study. The lectures were given under the following headings: Physiological principles displayed in the evolution of the mammalian circulation; Establishment and characteristics of the capillary circulation; Appearance and elaboration of lymphatic vessels; Blood, tissue fluid, and lymph as illustrated by experiments upon the heart and lungs; Relations of the lymphatic system to practical problems in surgery and medicine.

The essential features of the relations of blood and lymph in mammals are listed as follows:

(1) A closed system of blood capillaries with endothelial walls of varied permeability but capable of retaining practically all of the blood plasma during the usual conditions of rapid capillary transit; (2) A variable hydrostatic pressure in the capillaries; (3) A mixture of extracellular nonrespiratory proteins in the blood to which the capillary endothelium is somewhat permeable; (4) An extravascular tissue fluid, lower than the blood plasma in content of blood proteins but in other respects practically identical with plasma; (5) A system of closed lymphatic capillaries with extremely permeable endothelial walls, which lacks any inherent propulsive mechanism to move lymph into larger valved vessels but is dependent upon inconstant and extraneous forces, such as those of muscular activity or massage, to cause entrance of fluid, cells, and particles into lymphatic capillaries and eventual flow of lymph back to the blood.

Drinker emphasizes that between fish, which present the most primitive expression of these essential features, and mammals, where there is the highest complexity, no new principles are disclosed. "One finds, particularly upon the side of the lymphatics, what seems to be a straightforward increase in complexity; and this in turn must rest upon greater and greater need for the lymphatic system." He believes that the solution of the appearance and elaboration of the lymphatic circulation can best be solved by experiments on fish. Function of the lymphatics cannot be isolated from that of the blood capillaries: "Both serve the same end—the maintenance of the internal environment at constant

composition and volume." In osmotic pressure of the plasma proteins, in infection, and in removal of foreign materials the lymphatics are effective, but their real usefulness "is nearly always to supplement reactions initiated in the blood capillaries and later in certain respects regulated through lymphatic absorption. They are functionally distinctive, but as part of a larger process—soldiers in an army whose individual performance may be arresting, but whose real accomplishments are inseparable from those of the army as a whole."

Introduction of microchemical methods made it possible to make repeated analyses of lymph from the same vessel. The problem of fat absorption is now capable of study since from small laboratory animals lymph and blood can be collected during periods of fat deprivation and fat feeding. It will perhaps ultimately be possible to trace the gradual steps in the development of one of the most specialized features—the villi—of the lymphatic system.

The volume is beautifully printed and illustrated. It is provided with a substantial bibliography but unfortunately there is no index. We strongly recommend this book for biological and medical school libraries.



FUNCTIONAL NEUROANATOMY.

By Wendell J. S. Krieg. *The Blakiston Company, Philadelphia.* \$6.50. 10½ x 7½; xx + 552; 1942.

This is a volume, comprising textbook, laboratory directions and atlas, which may profitably find its way to the desks of many students. From several points of view it is highly superior to comparable existing treatises for the beginning student. In the first place, in the case of each functional system a clear and relevant discussion of the structure and function of the peripheral nerves and sense organs is included. This, although frequently only briefly reviewed in neurology because of the student's supposed familiarity with it from gross anatomy, is extremely welcome here since the student is enabled to coordinate it intelligently with his knowledge of the related central parts. Second, the book contains lucid discussions of many functional aspects of neurology which are often available only in textbooks of physiology, but which do well to share the pages in which the related anatomy is described. Finally, a number of new and highly original illustrations are included which demonstrate vividly many points that are nowhere else in print so clearly illuminated. The figures are especially fine in the case of gross dissections and of reconstructions demonstrating topographical relationships. Some students will find helpful the three-dimensional interpretations of the atlas drawings.

Constructed according to the principles of functional systems, the work as a whole is often not tightly enough organized in detail to complete successfully the whole discussion of a system within a single unified section, and, therefore, in this respect it is less useful than some

of the texts already available. Furthermore, the treatment of actual fiber-tract connections in both text and illustration is less satisfactorily handled and is less clear than much of the other material presented. The book as a whole, therefore, serves as an excellent and desirable supplement to already existing textbooks, rather than as a substitute for them.

If a reviewer dares hazard a few suggestions to an author who states in the preface of his work that he has "satisfied himself that he cannot materially improve on it, either in content or form," the following points may be mentioned. The double use of the word *thalamus*, both as an approximate synonym for *diencephalon* and also in its normal sense to describe the thalamus proper, is sure to be confusing to beginning students. Controversial issues (e.g. macular sparing, ipsilateral motor representation in the cortex, classification and localization of speech or language mechanisms, etc.) are not always judiciously treated. Stereograms designating the planes of section are omitted only for the very portions of the atlas where the beginning student has most need of them, namely, the brain-stem anterior to the midbrain, where the sections are in a plane intermediate between transverse and frontal.

The book is magnificently printed, but there are some bad typographical errors and one tantalizing pun—*re* the "Procrustean six layers" of the cortex.



A TEXTBOOK OF HISTOLOGY. *Fourth Edition, Completely Revised.*

By Alexander A. Maximow and William Bloom. W. B. Saunders Company, Philadelphia and London. \$7.00. 9½ x 6½; xv + 695; 1942.

Reviews of the three previous editions of this book have appeared in Vol. 6, p. 242, Vol. 10, p. 110 and Vol. 14, p. 93 of this journal. Slight additions have been made in most of the chapters in order to bring the material up to date. A section on the history of histological methods has been added to the introduction and recently developed techniques are included. The section on the composition and structure of protoplasm has been rewritten by R. R. Bensley. The sections on histogenesis and repair in the chapter on bone, the sections on the aortic and carotid bodies in the chapter on the blood vascular system, and the sections on the white pulp, and the union of arteries and veins in the chapter on the spleen contain slight changes and additions, as do the sections on the thyroid, the parathyroid, the pancreas and the skin. The section on the neuron doctrine in the chapter on nervous tissue has been rewritten by S. Polyak, who has also condensed and revised the section on the retina in the chapter on the eye. In the chapter on the female genital system, the sections dealing with the endometrium of the uterus, its cycle and endocrine correlations, and in structure in early pregnancy have been extensively revised and supple-

mented by G. W. Bartelmez. The illustrations have been increased by 35 new figures, bringing the total number to 562. However, the majority of the changes which have been cited are of a minor nature. This comprehensive book is to be highly recommended for the use of medical and pre-medical students, and is a valuable reference for any teacher in the biological sciences.



A TEXT-BOOK OF NEURO-ANATOMY. *Third Edition, Thoroughly Revised.*

By Albert Kuntz. Lea and Febiger, Philadelphia. \$6.00 net. 9½ x 5½; 518; 1942.

This new edition of one of the more popular text-books of neuro-anatomy has not undergone drastic alteration. Certain chapters, however, particularly those dealing with the diencephalon and the structure of the cerebral cortex, have been extensively revised and rewritten so as to include the newer literature dealing with these regions.

Numerous figures have been replaced by new ones, but some of the illustrations still leave much to be desired. The absence of a comprehensive, systematically arranged series of representative cross-sections is regrettable; for such a series is almost indispensable to the beginning student, who will be the chief user of this publication.

The chapter on the autonomic nervous system remains one of the outstanding features of the book. It should continue to be of great value to the student in correlating the gross and microscopic features of this important part of the nervous system.



PHYSIOLOGY AND PATHOLOGY

MEMORANDA ON MEDICAL DISEASES IN TROPICAL AND SUB-TROPICAL AREAS.

The War Office. Reprinted by permission of the Controller of His Britannic Majesty's Stationery Office. Chemical Publishing Company, Brooklyn. \$4.75. 8½ x 5½; 282; 1942.

This is indeed a practical book for one who is concerned with tropical and sub-tropical diseases and desires a source of authoritative information. The information that is compiled has been obtained from the experiences of army medical officers who have actually encountered the diseases under war conditions. Fortunately the non-essentials have been omitted in order to make it a small book that one would not hesitate to include among his limited equipment.

As is stated in its preface, the book does not cover the whole range of tropical medicine. There are a number of relatively rare diseases which might be encountered in the tropics about which the book has nothing to

relate. Nevertheless the fact that this is the sixth edition of the *Memoranda*, indicates that it has proved to be a handy manual for use in the field. The diseases that are discussed are not limited to those produced by one or two general types of etiological agents, but the most frequently encountered tropical diseases are discussed regardless of the agents or conditions that cause them. For instance, diseases caused by infection with worms, protozoa, fungi, bacteria and filterable viruses are included along with a consideration of arthropod pests, heat-stroke and vitamin deficiencies.

The subject matter is well organized and written in an interesting style. After a brief introductory statement concerning a disease, its etiology, symptoms, complications, diagnosis, differential diagnosis, prophylaxis and treatment are presented usually in the order named. The most valuable portion of the discussion usually concerns the symptoms and the treatment of the disease. The symptoms are described fully and in vivid detail, as is possible only by those who have had frequent experience with the disease. Various types of treatment are presented; the ideal treatment where time, equipment and supplies are not problems on down to the emergency first aid that may be all that can be given during active combat.

In the appendix, the International Rules of Zoological Nomenclature are presented with the hope that they might be helpful to the medical officer in writing reports concerning animal parasites. The text is well illustrated with drawings, photographs, and reproductions of fever charts. In addition to the list of contents, an index is also included.



AMBASSADORS IN WHITE. *The Story of American Tropical Medicine.*

By Charles Morrow Wilson. Henry Holt and Company, New York. \$3.50. 9½ x 6; x + 372; 1942.

Wilson has effectively brought to the attention of the general reader what has long been known to the public health officer—the great battle yet to be fought in Latin America to combat the deadly toll of infectious diseases.

There are somewhere around a hundred and twenty million people in Latin America, from the Rio Grande to Cape Horn. At this very moment it is a good bet that at least fifty million of them are sick. Sick of everything from sprue to leprosy. Sick of almost all the diseases that we in the United States encounter in our own lives, and of a multitude of savage and highly fatal diseases about which we know almost nothing.

Tuberculosis is to-day the deadliest of tropical diseases, with influenza-pneumonia, malaria, diarrhea-enteritis, diphtheria, infantile paralysis, typhoid, and meningitis following in decreasing order. Excluding cancer, which is fifth on the list of the ten main causes of death, and heart disease, which is ninth, the eight

remaining principal sources of fatality are the result of hostile organisms. "Sickness in Latin America," says Wilson, "is as much a condition of life as weather or food. Even yet we are far from understanding what fifty million sick people mean. They signify a society of sick men."

Widespread illness does not mean that our neighboring countries are not carrying on a valiant battle against disease. The problem is one of great magnitude and complexity. Large sections of the population are in the midst of vast expanses of jungle, mountain, and desert, or beyond such regions out of communication with more progressive peoples. Scarcity of communication, clinical facilities and modern equipment, lack of independent medical practitioners, illiteracy and poverty among large groups of the inhabitants coupled with racial prejudices all have a part in making the fight to eradicate disease a difficult one.

It is a stirring story that Wilson tells of the great battles that have already taken place against tropical disease and of the men—Finlay, Walter Reed, Gorgas, Deeks, Noguchi and many others—who have served in the fight, also of the work of the United Fruit Company, The Rockefeller Institution and other organized groups. His statements are supported with bibliographical notes for each chapter (grouped together at the end of the text). A general bibliography of 149 titles and a chronological list of Latin American epidemics are given in the two appendices and the volume is carefully indexed.



FAMILY FOOD CONSUMPTION AND DIETARY LEVELS. Five Regions. U. S. Department of Agriculture, Miscellaneous Publication No. 452. Consumer Purchases Study. Urban and Village Series.

By Hazel K. Siebeling, Day Monroe, Esther F. Phippard, Sadye F. Adelson and Faith Clark. Government Printing Office, Washington. 30 cents. 9½ x 5½; iv + 268; 1941 (paper).

Food consumption is a subject of universal and perennial interest. About half of the income of families in the lowest third of the income scale goes for food. Even those in the highest third put more than a fifth of their incomes into this item of the budget. The way food money is spent, the choices that families make, is of much concern to all interested in human welfare; there is a close relationship between dietary adequacy and health. Producers also have an interest in the volume and kind of food eaten by the population. Such facts bear directly on the activities and incomes of farmers, workers in food industries, and persons engaged in transportation and other distributive services.

The main requirements for eligibility of families for this survey were: families to include a husband and wife, both native-born; the husband and wife to have been married at least a year and to have kept house in the community studied for at least 9 months of the report

year: white families, except in the Southeast, and in New York City and Columbus, Ohio, where a separate study (included in this report) of Negroes was made; no family to have had the equivalent of more than one roomer and/or boarder for 52 weeks of the report year and no family to have received relief during that period. These requirements together with other minor requirements threw families into the study group that were generally in better circumstances than those omitted from the study. Therefore, the authors point out that the "differences between the groups studied and the total population should be recognized in using the expenditure and consumption data of this volume."

The report includes money value of food in a 12-month period, dietary patterns as shown by 7-day schedules, human requirements for nutrients as discussed in this report, nutritive value of diets in relation to money value of food, nutritive value of diets in relation to degree of urbanization and region, classification of diets by grade, etc. This part of the report covers 73 pages. The remaining 191 pages are taken up with four appendixes concerned with table titles, legends for the figures, tables, methodology and appraisal, and glossary.



ANNUAL REVIEW OF PHYSIOLOGY. Volume IV.

Edited by James M. Luck and Victor E. Hall. *Annual Reviews, Inc. Stanford University, P. O., Calif.* \$5.00. 8½ x 5½; vii + 709; 1942.

The *Annual Review of Physiology* has rightly come to fill an indispensable place in the reading of a great number of general biologists as well as physiologists. This volume is no exception. The articles are of the same general type as in previous editions, giving very brief but authoritative summaries of the current work in various active fields of physiological investigation. The majority of articles are on topics which have been covered regularly by this review and, in these, most of the works cited are limited to the period of 1940 to early 1941. Chapters on topics not recently included in this review also contain references to older research. Because of war conditions the material covered is largely by Americans, but foreign papers have been included as they have become available.

The volume contains sections on Permeability, Physiological effects of neutron rays, Physiological aspects of genetics, Developmental physiology, Water metabolism, Growth, Energy metabolism, The physiology of the skin, The peripheral circulation, Heart, Blood, The digestive system, Kidney, Electrophysiology, The spinal cord and reflex action, The central nervous system, The autonomic nervous system, Sense organs, Metabolic functions of the endocrine glands, The physiology of reproduction, Physiological psychology, Applied physiology, and The pharmacology of drug addiction.

The subjects of water metabolism and pharmacology of drug addiction appear for the first time in this *Annual* and those of permeability and applied physiology appear for the first time since 1939. The latter is quite different from the first presentation of this subject, and deals almost entirely with pressure effects as they are involved in aviation and submarine work. Military secrecy prohibits the publication of much of the recent work dealing with these problems, but the authors of this section were able to review a considerable volume of valuable work and their discussion does much to draw attention to the many problems in this field which demand immediate attention.

Each section of the book is provided with a comprehensive bibliography and there are complete author and subject indexes.



TEXTBOOK OF CLINICAL PARASITOLOGY: Including Laboratory Identification and Technic.

By David L. Belding. *D. Appleton-Century Co., New York and London.* \$8.50. 9½ x 6½; xxi + 888; 1942.

As inferred by the title, this textbook places emphasis upon the clinical aspects of parasitology. It seems to possess all the information necessary for a physician to diagnose and treat parasitic diseases successfully. In spite of this primary interest, the book also presents the zoological background of the parasites without which a more complete understanding of the diseases would be impossible. Experience has demonstrated that successful prevention and control are only possible through the application of a well-rounded knowledge of the subject. Such a knowledge can be acquired through a study of this book.

The most outstanding feature of the volume is the frequent use of charts and diagrams for presenting various types of data. For instance, they are used to graphically present life cycles, geographical distribution, pathology, symptomatology, treatment, classification, and morphology. They are not presented to take the place of descriptive text, but serve as clear, concise summaries and readily available sources of information. The student will find them a great help while endeavoring to acquire the fundamental facts. Others will find them equally helpful for refreshing their memories on subjects studied in the past.

The protozoa, helminths, and arthropods that cause human diseases are discussed in the order named. Some of the closely related parasites of lower animals are also included. The first several chapters are devoted to parasitism in general and the frequent relationships that exist between the parasite and the host. The last section of the book presents the technical methods for the diagnosis and treatment of parasitic infections. This section is well organized and should prove to be a help to one actively engaged in these phases of the subject. In addition to the bibliography, references to

the original literature are conveniently placed at the end of each chapter. Both a subject and an authors' index are included.



OUTLINES OF FOOD TECHNOLOGY.

By Harry W. von Loesecke. Reinhold Publishing Company, New York. \$7.00. 9 x 6; 505; 1942.

The beginning of the modern food industry dates back to the era of Pasteur with the overthrow of the theory of spontaneous generation. Up to about 100 years ago salting, drying, and, to a much less degree, chilling were the only known methods assuring the prolonged preservation of food. Within more or less of a century what is probably the greatest industry in the world, the production, preservation, and shipping of food, has developed.

The money spent in obtaining food far exceeds that for any other purpose. The number of people gainfully employed in supplying the world with food is greater than any other occupation. The farmer raises his crops and livestock which he turns over to thousands of others to market. To convert these materials into raw food products many thousands more are employed in canning, baking, confectionery making, sugar refining, wholesale and storage warehouses, stores, hotels and restaurants. To this vast army may be added those employed in manufacturing dishes, silverware, machinery for processing foods, bottles, cans, cartons and thousands of other accessories indispensable to the food industry.

In the present volume von Loesecke has described briefly the more important processes in food production. Even with such a limitation—omitting all detailed descriptions of the preparation of the different food materials or the appraisal of nutrient values and the inclusion of only a minimum of statistical data—the volume contains an enormous amount of informative material. The usefulness of the volume is extended by the carefully prepared “suggested readings” list accompanying each chapter. The subject matter is divided as follows: tin and glass container; fruits and their products; canning of vegetables; dairy products; meat, meat products and poultry; fish and shellfish; grains and their products; edible fats and oils; sugars and starches; nuts; spices, relishes, essential oils, and extracts; beverages; confectionery, jams, jellies, preserves and certified dyes; storage and marketing of fruits and vegetables; and preservation of foods by freezing. The volume is well illustrated and indexed.



THE COMPLETE BOOK OF DIETS FOR ALL AGES INCLUDING MEDICAL DIETETIC SUGGESTIONS FOR 325 COMMON AILMENTS.

By Richard M. Field. Doubleday, Doran and Company, New York. \$2.50. 8 x 5½; liv + 272; 1942.

The author's 25 years of successful medical practice, as well as his recent experience in formulating corrective dietary charts and serving as an authoritative adviser and consultant on matters pertaining to diet in relation to health and disease, have well qualified him for the task of preparing this comprehensive work. Although intended primarily for use by the general practitioner, the book is written clearly and simply enough to be profitably used by the intelligent layman.

Part I of the volume lists the nutritional requirements for man at various ages and suggests 8 normal diets to be followed under conditions of normal health. Listed also are 24 corrective diets suggested for the cure or treatment of some 325 common ailments. Throughout this section, the author emphasizes the fact that diet alone, without the supplemental aid of good hygiene, mental and emotional stability, and freedom from the multitude of modern worries, cannot bring miraculous cures over night. Stress is also placed on the fact that most people of our day resist any attempt on the part of the physician to tell them what they *must* and *must not* do, and that the best way for the physician to achieve the desired result is to hand them a list of suggestions.

Part II of the book deals with the recent (1941-42) trends in balanced nutrition. There is a plea for common sense in balancing meals; a complete debunking of many overrated commercial products having a direct bearing on nutrition; and some sound advice on the selection of many food products.

The work is authoritative and up-to-date, and as such, it will undoubtedly find a welcome place on the library shelves of many general practitioners as well as nutrition-conscious laymen.



SUPERIOR CHILDREN THROUGH MODERN NUTRITION. *How to Perfect the Growth and Development of Your Children from Birth to Maturity.*

By I. Newton Kugelmass. E. P. Dutton and Company, New York. \$3.50. 8½ x 5½; xiv + 332; 1942.

The purpose of this book is to help parents perfect the growth and development of their infants and children. It grew out of the application of the newer knowledge of nutrition in the pediatric practice of the author. One of the outstanding features of the volume is the recognition that no two children are alike—that all children do not respond with equal benefit to a “well-balanced diet for the average child.” The author takes into consideration the body-build, age and mental attitude of the child so that parents can pick out the proper combinations and prepare the kind of meals that will be consumed with utmost benefit for physical and mental growth to maturity. The following subjects are discussed: modern materials of life, energy and vitamin foods, minerals as protective foods, nutrition for superior growth, individualized newborn, breast and artificial

feeding, mixed feeding, food allergy, feeding behavior, dietary needs of every age, feeding according to body build, preventing constipation, safeguards for economical living, helping lean and fat children, and vitamin values of common foods. A helpful feature of the book is the "questions and answers" which are appended to most of the chapters. Complete tables of vitamins and minerals are included with instructions as to how much of each should be given and in what form each is most effective. Even the costs of these health-builders are considered in the author's recommendations.

This excellent book is recommended to parents and to school, camp, hospital, Red Cross, and day-nursery officials who may not have the time or the opportunity to study the technical aspects of nutrition. It should be widely accepted.



MODERN MEDICINE: Its Progress and Opportunities.

Netta W. Wilson and S. A. Weisman. George W. Stewart, Publisher, New York. \$2.00. 8 x 5½; vi + 218; 1942.

This is the sort of book which this reviewer believes should be in every family library for it contains the authoritative information that all intelligent and well-informed laymen like to have about the important aspects of modern medicine. The main ideas, the great discoveries, the cures, and the personalities that have advanced the practice of medicine all are recounted here. The chief problems that modern medicine is trying to solve, other problems that have been solved in the past, the most recent developments in medical theory and practice, and the opportunities for careers that should especially interest young men and women are all discussed completely by the authors. The stories of bacteria, virus diseases, animal parasites of man, vaccines and serums, animal experimentation, the heart and some of its diseases, the blood and some of its diseases, tuberculosis, cancer, surgery, anaesthesia, the endocrine glands, and nutrition are all told in succession in a most entertaining and instructive manner. The book concludes with a chapter on "Modern medicine looks forward." Appended to the volume are a comprehensive list of books to read about modern medicine and a complete index.

This book is heartily recommended to all those adults, young and old, who have a normal interest in science and in the world about them but who know nothing technical or detailed about human physiology and the intricacies of modern medical practice.



RABIES.

By Leslie T. Webster. The Macmillan Company, New York. \$1.75. 8 x 5½; vi + 168; 1942.

With rabies becoming more and more a community

problem the public is demanding information on two cardinal points: how rabies is diagnosed and how rabies can be controlled. The author feels that there is definite need for some treatise on rabies, critical, fairly inclusive, but simple and available to all. This book is an attempt to fill that need. Since the questions of diagnosis and prevention seem uppermost in the minds of most inquirers the author focuses the subject matter on these two problems. Quantitative data and present concepts are stressed rather than original observations and the chronological development of ideas. In addition to a long-needed survey of the available literature on rabies, the author gives a detailed report of the Rockefeller Institute's "mouse tests" for diagnosis and for evaluating rabies vaccines. The discussion includes: rabies in animals and in man, the cause, diagnosis, history and epidemiology of rabies, and the prevention of rabies prior to and following exposure. There is a complete bibliography and a comprehensive index provided. The appendix contains information relative to the disposal of rabid and of vicious dogs, confining animals to prevent spread of the disease, rabies antibodies and their relation to immunity, and immunizing potency of antirabies vaccines.

This volume will prove useful to the dog owner and general public, and indispensable to those engaged in rabies research, to doctors and veterinarians, and to public health administrators.



INTIMATE BACTERIOLOGY: A Text and Laboratory Manual.

By Casper I. Nelson. Burgess Publishing Company, Minneapolis. \$2.50. 10½ x 8½; v + 166; 1942.

Designed for use in the teaching of continuation classes in general bacteriology, the plan of this combination text and laboratory manual is to present the relationship of bacteria to the human body from the very beginning of the individual's existence to old age and death. This it does in a very commendable and novel fashion. Some of the more interesting chapter headings have to do with: prenatal infections, bacterial flora of the intestinal tract, weaning, constipation, use and abuse of cathartics, correction of health through diet, food poisoning, public sanitary services, the disposal of sewage and its relationship to public health, the respiratory tract, children's diseases, the skin and hair, and immunity and allergy. In the section of the book devoted to laboratory exercises, complete descriptions and directions are provided for a semester's work in the laboratory—with many of the standard exercises available along with a number of interesting new ones. References are given as footnotes throughout the book. There is no index. The book is illustrated with a number of drawings.

The volume is recommended for that group of students who, having been intrigued by a general course in

microbiology, would like to learn just a little more with special regard to self-application, but do not necessarily wish to follow into the field of medicine. For them, this method of presentation should hold their interest in a natural and effective way.



THE CONQUEST OF BACTERIA *from Salvarsan to Sulphapyridine.*

By F. Sherwood Taylor. Foreword by Henry E. Sigerist. *Philosophical Library and Alliance Book Corporation, New York.* \$2.00 8½ x 5½; 178; 1942. This book, written by one of England's most eminent scientists, is the story of the chemical discoveries which conquered disease, and of the men behind these conquests. The appeal of the volume is quite definitely to the layman who is interested in reading a fascinating study of a subject heretofore reserved mainly for the specialist. The author discusses in order: bacteria and disease, the body's defenses, the development of drugs, the rise of chemotherapy, prontosil, the sulphonamide group of drugs, sulphonamides and *Streptococcus pyogenes*, pneumonia and M and B 693, further triumphs—including limitations of treatment and mode of action—and, finally, the need for continued research, including material on the present expenditure of public money on health services and on research, the present state of research, and the work of the various pharmaceutical firms in relation to chemotherapeutic research. There is no bibliography, but a comprehensive index is available. There is also a table of the various sulphonamide drugs.

Many readers will find this the best type of popular book on a scientific subject, and it should be warmly received by the thousands of people who have read accounts of the new miracle drugs and who would like to know the latest developments concerning them, as well as something about their interesting history.



THE 1941 YEAR BOOK OF GENERAL MEDICINE.

Edited by George F. Dick, J. Burns Amberson, George R. Minot, William B. Castle, William D. Stroud and George B. Eusterman. *The Year Book Publishers, Chicago.* \$3.00. 7 x 4½; 848; 1941.

The merits of this group of the well-known "Year Book Series" are sufficiently wide-spread to obviate the necessity of saying much about the book. The subject matter is divided into five sections: infectious diseases, diseases of the chest, of the blood and blood-forming organs, of the heart and blood vessels, and of the digestive system. The distinguished editors of the volume have examined the voluminous literature in the above-mentioned five fields of general medicine and have selected the more important and more promising articles which are here collected and published in one volume of

850 pages for the reference use of the general practitioner, the medical student, and the seasoned investigator, to all of whom this book should prove indispensable. Here are recorded the latest developments in: sulfonamide therapy, pneumonia, tuberculosis, pneumoconiosis, anemias, nephritis, electrocardiography, diabetes, vitamin nutrition, hemophilia, hypertension and poliomyelitis—to mention only a few of the subjects considered. The book is illustrated with numerous photographs, drawings, charts, tables and graphs, and there is a complete index of the subject-matter, as well as an index to the authors represented.



INTRODUCTION OF HUMAN PHYSIOLOGY. *Third Edition, Revised.*

By Lathan A. Crandall. W. B. Saunders Company, Philadelphia and London. \$2.25. 7½ x 5½; xii + 388; 1942.

This little volume is recommended for introductory courses in physiology for college students and nurses. The most essential phases of the vast modern science of physiology have been selected and presented in the simplest possible fashion with often more attention to the practical than to the theoretical aspects of the subject matter.

The book was first written in 1934. For this third edition the author has added a new chapter on nutrition and has extensively revised the sections dealing with metabolism, the function of capillaries, etc. In order to be up-to-date he also gives considerable space to a discussion of the problems of respiration in relation to high altitude flying. Most of the 113 illustrations are well chosen and very helpful to the reader, but some are not clearly reproduced or else too much reduced in size.

There is a good glossary, an adequate index and a very brief list of references for additional reading. Precisely because this book is intended for beginners, a chapter outlining the historical development of physiology would have been desirable at least to indicate that we are still in the midst of rapid advances in the full understanding of the real functions of our bodily structures and their manifold interrelations.



THE PHYSIOLOGY OF DOMESTIC ANIMALS: with a Chapter on The Physico-Chemical Basis of Physiological Phenomena, by E. A. Hewitt: *A Part on the Endocrine Organs and Reproduction,* revised by S. A. Asdell. *Fifth Edition, Revised.*

By H. H. Dukes. Foreword by H. D. Bergman. Comstock Publishing Company, Ithaca. \$6.00. 9 x 6; xiv + 721; 1942.

The present edition, the fifth since the volume first appeared in 1932, has been revised and much of it completely rewritten. A number of subjects have been

added, such as a chapter on digestion in the chicken, sections of respiration in birds, urine of the chicken, reproduction in the fowl, and physiological oxidations. The material on the endocrine organs has been merged with the part on reproduction under the heading "The endocrine organs and reproduction." Much of the anatomical material in the part on the nervous system has been deleted in the present edition and many changes have been made in the illustrations.

Originally designed for students of veterinary medicine, with the extensive revision and up-to-date presentation of the subject, the usefulness of the volume extends to workers in animal husbandry and practitioners of veterinary medicine. The volume will also be found invaluable in those biological laboratories where there is much experimental work with animals.



FOOD VALUES IN SHARES AND WEIGHTS.

By Clara Mae Taylor. *The Macmillan Company, New York.* \$1.50. 9½ x 7; 92; 1942.

Out of the recent nutrition-consciousness of America has arisen the need for just such a handbook as the one under review. For the layman who wants to know the relative values of various foods as regards their nutritional components, as well as the minimal nutritional requirements for normal health and vitality, this book will undoubtedly prove to be both valuable and popular.

After a brief discussion of the minimal daily nutritional requirements of the human body in terms of calories, proteins, calcium, iron, vitamin A, thiamin, ascorbic acid, and riboflavin, (30 shares of each are designated as the daily requirement for a moderately active man) the work lists, in Table II, some 500 dietary items showing the number of shares derived from a given quantity of food, and in Table IV, the same dietary items giving the food values in weights. There is a brief graphic presentation of the comparative nutritive value of several foods. Space is provided for recording calculations of food intake for one day in terms of shares, weights, and menus.

The work carries a bibliography of 15 titles.



THE 1941 YEAR BOOK OF PUBLIC HEALTH.

Edited by J. C. Geiger. *The Year Book Publishers, Chicago.* \$3.00. 7 x 4½; 544; 1942.

Under the following headings Geiger has grouped the summarized material which he has selected from a large number of journals as being outstanding for the year and of greatest usefulness to his readers: medical care, child hygiene, communicable diseases and epidemiology (4 divisions), dental hygiene, food and milk, health education, hospital hygiene, housing, industrial hygiene, laboratory, maternal care, mental hygiene, military hygiene, nursing, nutrition, and statistical.

Many of the articles are accompanied by brief editorial notes (in small type), and in some instances figures and tables have been included. There is a general index and one of authors. A handy volume which will well serve the busy public health worker as well as others interested in contemporary public health developments.



BIOCHEMISTRY

A SYMPOSIUM ON RESPIRATORY ENZYMES.

By Eric G. Ball, Fritz Lipmann, Kurt G. Stern, Fritz Schlenk, et al. *University of Wisconsin Press, Madison.* \$3.00. 9½ x 6; xii + 281; 1942.

The extremely rapid advances which have been made in our knowledge of enzymes and their action during the past few years have made it practically impossible for most biologists to keep up with the voluminous literature on this subject. However, a knowledge of enzyme chemistry is increasingly important in interpreting and evaluating other biological data. Reviews of the nature of this symposium are therefore extremely valuable to the general biologist as well as to the enzyme specialist.

This book represents a compilation of the most recent facts and theories dealing with the particularly important enzymes of respiration and intermediary metabolism by 27 contributors including many of the most active American investigators in the field. The Foreword states that the symposium was primarily designed to discuss the interrelations of vitamins and enzymes, but respiratory enzymes not directly correlated with vitamin action are also included. This is necessary to give a well-rounded picture of the subject, as it would be impossible to consider the pyridine nucleotides or flavoproteins as systems isolated from respiration in general.

The contributors include theory and speculation as well as established fact in their papers and differences of opinion on such issues as the citric acid cycle and the "by-passing" of the cytochrome system present points of view to be evaluated by the reader. The considerable emphasis placed on the unsolved problems in the field gives the book added value to those who are actively interested in the problems of respiration.

Each article is accompanied by a good bibliography. In view of the tremendous volume of literature on this subject, these can hardly claim to be complete, but they do represent the most pertinent articles and provide a suitable starting point for anyone wishing to investigate a particular problem more thoroughly. There is no index, but the very complete table of contents makes the material readily available for reference.

There can be little question but that this book will adequately fill the need for a concise and authoritative review of our present knowledge concerning respiratory enzymes in both normal and pathological tissues. It should be of value both to the biochemist and to the

general biologist striving to keep abreast of this rapidly expanding field.



FROM WITCHCRAFT TO CHEMOTHERAPY. *The Linacre Lecture 1941.*

By Sir Walter Langdon-Brown. Cambridge, at the University Press. 60 cents. 7½ x 4¾; 60; 1941 (paper).

To comprehend witchcraft Langdon-Brown says that "we must see it as an expression of the thwarted instinctive self turned renegade and forcing its way into consciousness again with an evil leer. Witchcraft and fertility rites had seized on the imagination of people thousands of years before the introduction of Christianity." Witchcraft he conceives to be "the persistent vestige of the old fertility religion." It is estimated that throughout Europe, within the space of 100 years, something like two million persons were burned as witches. That in the 17th century such persons as Sir Thomas Browne, Henry More, and Joseph Glanvill believed in witches was due probably to the fact that to doubt the existence of evil spirits implied an equal doubt in the existence of beneficent spiritual forces.

The widespread use of drugs and poisons in the magic rituals led empirically to the discovery of the therapeutic value of many of these. It is estimated that 137 modern botanical remedies undoubtedly emanated from folk-medicine, and that 25 probably and 17 possibly did. The author lists briefly the supposed characteristics and virtues of the following: mandrake, poppy, aconite from monkshood, and conium from hemlock, cinchona and mistletoe, wormwood, chamomile, scurvey grass, digitalis, and valerian. It was not until the end of the 18th century with the revolution in chemistry that pharmacology could properly evaluate these and similar herbs and drugs. But the great change was not to come until a century later with the discovery of endocrines, anti-toxins, vitamins, and X-rays and radium, all within a comparatively brief period. Then began the era of chemotherapy "the last great triumph of therapeutics."



A SIMPLIFIED SYSTEM OF ORGANIC IDENTIFICATION.

By J. L. B. Smith. Chemical Publishing Company, Brooklyn. \$1.50. 8½ x 5½; 48; 1942.

The scheme presented in this workbook uses to the utmost the simple, practical, and time-saving taste, odor, color, and reaction tests in identifying a large number of organic compounds, and is completely devoid of the theoretical principles and detailed formulae inherent in most organic texts. The work is set up in the form of a key, using generally a binomial system to describe progressive reactions; e.g. "neutral or only faintly acid vs. distinctly acid"; "immediate pink color vs. no bright pink color"; "insoluble vs. soluble"; etc.

Except for the alkaloids and dyestuffs, the manual covers a range of material (some 250 individual compounds) which more than meets the requirements for the A.B. degree, and with suitable selection and eliminations, can be adapted to meet the needs of many college class levels. The value of this revolutionary method of presentation is attested by the success with which it has been employed by the author for a number of years in his classes at Rhodes University College, Grahamstown, South Africa.

An appendix listing the composition and strength of a number of reagent solutions, and a complete index are provided.



BIBLIOGRAPHY OF REFERENCES TO THE LITERATURE ON THE MINOR ELEMENTS AND THEIR RELATION TO ANIMAL NUTRITION. *Third Supplement to the Third Edition.*

Originally compiled by L. G. Willis. Chilean Nitrate Educational Bureau, New York. Free. 11 x 8½; 78; 1942 (paper).



SEX

SEX GUIDANCE IN FAMILY LIFE EDUCATION. *A Handbook for the Schools.*

By Frances Bruce Strain. The Macmillan Company, New York. \$2.25. 8 x 5½; viii + 340; 1942.

Mrs. Strain's wide experience in sex education has well fitted her to write the present book. It is designed for the use of the teacher. The author emphasizes the need for a long range program in sex education in schools through all the grades from primary to junior and senior high schools. That there is need for such a program, especially during the present conditions of war with the accompanying disorganization of homelife there seems little doubt. There is far more in sex teaching than the simple facts of mating, fertilization, and birth of human beings, as Mrs. Strain clearly shows. Many of these divergent problems can be more naturally dealt with in the school than in the house, but sex education should really be "a matter of cooperation between home and school, each doing its part."

It is recommended that the terms and phrases which belong to past thinking be abandoned.

There is the king-word itself, 'Sex', weighted with all the bias and calumny of centuries . . . Yet how difficult it is to replace.

In the upper grades where the program has crystallized into a definite entity, a name for the study would give significance and prestige. 'Human Relationships,' 'Family Living,' 'Preparation for Marriage' are all appropriate for a year's or a semester's course of study.

Sex Guidance is the chronicle of the unfolding of a child's sexual nature from the first days of his entrance

into school to the last before graduation. In the observation of this unfolding, a teacher will come to find many of the partitions and boundaries in her mind shifting or disappearing altogether. She will find that much conduct which appears to be sexual is social, and much that is social is sexual, that affection often wears the mask of cruelty, and cruelty the mask of affection. The sex education student today will need to be not only a biologist but a psychologist. He must be as much concerned with the dynamics of social and emotional growth as with reproduction, as skilled in interpretation of conduct as of chromosomes and the Mendelian Law.

We strongly recommend this book to all teachers whether it is their lot to take part in a program for sex education or not. It carries much wisdom and sensible advice for which all who have to do with young people will be grateful.



MICE, MEN, AND ELEPHANTS; *A Book about the Mammals.*

By Herbert S. Zim. Illustrated with Drawings by James Macdonald and with Photographs. Harcourt, Brace and Company, New York. \$2.00. 8½ x 5½; 213; 1942.

The problem of instruction in sex and its allied fields is probably one of the most difficult tasks in secondary education and the techniques of presenting this information are indeed numerous and varied. In this very simply written little book about the mammals the author, a teacher of science, has endeavored to answer the questions which he has found from his own experience uppermost in the minds of several thousands of his pupils—questions about themselves and other animals. Instead of giving isolated answers he has tried to fit them into their place in the general scheme of things. For example, he leads up to the principal facts about reproduction in man by first describing the general plan followed by all mammals from the smallest to the largest, and then points out the differences in the details of this plan found among the various types of mammals, including man.

"When you know more about your relatives, the mammals, and how they live, you will understand more about yourself—about the parts of your own body, what they are for, and how they work."

The book is illustrated with photographs and drawings.



BIOMETRY

ANNUAL BULLETIN OF VITAL STATISTICS FOR THE YEAR 1940. Including Summary Vital Statistics for 1921-1940.

State of Tennessee Department of Public Health. Nashville, Tennessee. 11 x 8½; 80; 1942 (paper).

In this bulletin are presented a summary of the vital statistics data for the year 1940 in relation to the data for previous years, summary tables with the data for the state for the 20 years, 1921-1940 inclusive, and detailed data for 1940 for the state, urban and rural areas, for the twelve cities with populations of 10,000 or more, and for the ninety-five counties in the state. The causes of death have been classified under the title numbers of the 1938 *Revision of the Manual of the International List of Causes of Death* used with the *Manual of Joint Causes of Death*. In the presentation of the data both recorded and resident data are shown. For the first time in 1940, a secondary or first contributory cause of death has been tabulated in addition to the usual primary cause. The present *Bulletin* contains five complete tables, giving information relative to: population, births, stillbirths, deaths, infant deaths, and maternal deaths—with rates. The principal causes of death in 1940 have been studied for five adult age groups with somewhat surprising results in the younger age groups. There is no index provided.



RESIDENT VITAL STATISTICS OF CITIES AND COUNTIES—NEW YORK STATE 1930-1939. *Births, Stillbirths, Infant Mortality, Deaths from Important Causes, and Cases of Certain Reportable Diseases.*

New York State Department of Health. Albany, N. Y. 9 x 5½; 135 + 3 maps. 1942 (paper).

The tables in this report show the basic vital statistics of New York State, New York City, and the rest of the State subdivided by counties, and places over 10,000 population in each of the years 1930-1939, and in the two five-year periods 1930-1934 and 1935-1939. The estimates of population are based on the federal censuses of 1930 and 1940. The statistics for areas in which state or federal institutions are located are exclusive of these institutions. All births have been allocated according to the usual place of residence of the mother. Cases and deaths from communicable diseases have been allocated to the place of origin of disease, and deaths from all other causes have been allocated to the usual place of residence. The rates for 1930-1934 and 1935-1939 are based not on annual averages but on the combined population and the total number of births and deaths for each of the five-year periods. In addition to the tabular material, certain data are included in pictorial form. There is no index provided.



THE BULLETIN OF MATHEMATICAL BIOPHYSICS. Volume 4, Number 4, December 1942.

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: An analysis of the shapes of a cell during division with particular

reference to the rôle of surface tension, by H. D. Landahl; Equilibrium shapes in non-uniform fields of concentration, by H. D. Landahl; Cellular forms: The tri-axial cell, by Alston S. Householder; The linear theory of neuron networks: The static problem, by Walter Pitts; Some problems in mathematical biophysics of visual perception and aesthetics, by N. Rashevsky.



PSYCHOLOGY AND BEHAVIOR

SENSATION AND PERCEPTION IN THE HISTORY OF EXPERIMENTAL PSYCHOLOGY.

By Edwin G. Boring. D. Appleton-Century Company, New York and London. \$5.00. 8½ x 5½; xv + 644; 1942.

This important book is a part of a larger plan. In 1924 the author had resolved to write a history of experimental psychology which should include an introductory account of the principal men and schools, to be followed by the main historical discussion of development in the various traditional fields of psychology. By 1929, however, the introduction on men and schools had become a sizable book in itself and this admirable work was then published under the title of *A History of Experimental Psychology*. By 1942, and in a somewhat similar fashion, the treatment of the vast literature in the traditional fields of sensation and perception became the present book. A third book may be written later on; this would present the experimental history of the remaining fields including emotion, learning, thinking, action, and attention.

The author writes that his histories are not historian's histories. "In both I have written solely to show how psychology came to be as it is now." This means that events which were outstanding in the past but not effective in shaping the present get little consideration. For instance, Weber's law and the nativism-empiricism controversy had both loomed large in the nineteenth century but they loom small today and in this book.

The first chapter deals, in historical perspective, with the general nature of sensation and perception, while the second is concerned with the physiology of sensation. There follow six long chapters devoted to visual matters and next come three substantial chapters on audition. These visual and auditory sections together comprise over one-half of the entire volume. Then follow the briefer treatments of the other sense fields. The next to the last chapter tells of the perception of time and motion while the final chapter is a brief and general analysis of the nature of scientific progress in relation to human thinking.

It is not surprising that the author was keenly alive to the difficulties and the responsibilities of his tasks of selection and presentation. He understood so well "how a mood that determined the choice of an after-

noon's exposition can fix the 'truth' of a certain matter upon graduate students for years to come." It was clear to him how personal interests or specialties tend to obtrude themselves unduly. He went to the original sources often to avoid the bias of rewritings. He used his guiding principle to write "solely to show how psychology came to be as it is now."

Unfortunately, Boring is not able to show just how or what psychology is now. He is powerfully motivated to do a good job, and it was for that very reason, perhaps, that caution caused him to revert to the tactic of 1929. At that time he wrote "a spindle-shaped history," one which deals with the half-century, 1860-1910, plus preceding developments and consequences. The more distant past was "tapered" and he felt unsafe about saying much regarding psychology since 1910. Exceptions were made in case of *Gestalt* psychology and behaviorism "because of the light that each casts backward upon the past." In the present volume the author seems satisfied up to 1920 at which time he starts to taper off or slow down. He stops at 1930, but again there are certain exceptions, this time most notable in the realm of audition.

We can understand the lack of perspective and the confusion of recency; the reluctance to crystallize in writing what still seems fluid. But in the case of this book on two of the most broadly important categories of psychology, much is lost by not carrying the exposition down to date. Recent material could have been duly qualified and subject to later revision, but it could have been as valuable and worthy as the recent reviews of special topics.

The content of this history is not limited on the side of recency alone. When the earlier work was written, the term experimental psychology meant "the generalized, human, normal, adult mind as revealed in the psychological laboratory." This meaning has been retained substantially in the present work, and the obvious result is a lack of much material in animal, abnormal, and child psychology—material which psychologists today call experimental. There is, to be sure, a limit to every literary effort, and this author has been conscientiously explicit regarding the limits of what has turned out to be a very fine book.

Each chapter ends with several pages of scholarly notes which not only add to the value of the text but also may serve as points of departure for further reading. There is a detailed index of subjects as well as an index of authors. The text is illustrated with 96 figures.



POETRY AND PROPHECY.

By N. Kershaw Chadwick. Cambridge, at the University Press; The Macmillan Company, New York. \$1.75. 7½ x 4½; xvi + 110; 1942.

The greatest cleavage plane in the human species is not

that between capital and labor, or that between the white and yellow races, or that between militarism and pacifism, for these antitheses, while they may disprove of each other, can at least understand each other. Often the capitalist began life as a laborer, and almost always the laborer has ambitions to become a capitalist. But between the general run of the population and those chosen few who have mystic experiences there is a great gulf fixed.

Within recent years there has been a renaissance of interest in mysticism. This is natural in view of the failure of those who consider themselves hardheaded practical men to make democracy safe for the world. The multitudes in the Vale of Decision have lost confidence in their leaders, and are lifting their eyes to the mountains for help. Under these circumstances it is not surprising that fake prophets have arisen and continue to arise, proclaiming divers and strange teachings, who claim access to ultimate reality by means other than the senses recognized by science. Probably there is no subject about which more egregious nonsense has been written, or which has been more deeply infested with charlatans, than mysticism.

But we cannot lightly dismiss *all* mystic phenomena as spurious. The well authenticated achievements in science of Emmanuel Swedenborg preclude the possibility of his having been mentally defective, and the works of Santa Teresa are not what we should expect from an imposter. Rather do they testify of her faith and remind us that "by their fruits shall ye know them."

Therefore an impartial, dispassionate scientific investigation of mystic phenomena seems urgent. But such would be attended with difficulty. One authority rather discourages the undertaking on the ground that the scientific method can apprehend no new truth, and that consequently another method is needed which can penetrate beyond the bounds of the proper field of scientific activity. Such a pessimistic appraisal of the capacity of the scientifically trained mind is fortunately not shared by the author of the book now under consideration.

Realizing that all scientific research must begin with facts, and that in this case sufficient facts are not available, the author has combed the written and the unwritten literature of the primitive peoples of three continents, making no assumptions, drawing no conclusions, but always laying foundations for further work. She finds no grounds for the popular belief that the shamans or medicine men of primitive cultures were mentally or physically unstable; on the other hand they are generally superior both mentally and culturally to the communities from which they come.

It is interesting to note that the word "mysticism" does not occur in the treatise. Yet the reader is likely to learn from this book more about the factors that produce mystic experiences than from many larger and more pretentious works which the reviewer might mention, and he hopes further works will issue from the

author's pen. After all, though mystic states may be essentially esoteric, there is no reason why knowledge about them should be.



THE VARIETIES OF TEMPERAMENT; *A Psychology of Constitutional Differences.*

By W. H. Sheldon, with the collaboration of S. S. Stevens. Harper and Brothers, New York. \$4.50. 9½ x 6; x + 520; 1942.

This is the second volume of a projected series of studies of constitution, the first one, *The Varieties of Human Physique*, appearing in 1940. The authors by statistical methods arrived at "three original clusters of traits" which were expanded to twenty traits each, the three groupings coming to represent polar mental constitutions and designated viscerotonia, somatotonia, and cerebrotonia respectively. Classical examples of these interesting types of temperament are measured on a quantitative 7 point scale, so that, for example, an extreme viscerotonic individual would have a rating of 7-0-0; in like manner an extreme somatotonic of 0-7-0, and a cerebrotonic 0-0-7. The basic data rests upon examinations, carried over several years, of 200 individuals, and whether by coincidence or because of more or less subconscious bias the three contrasting temperaments finally turn out to have some relationship to the somatypes described in the first volume and referred to as endomorphy, mesomorphy, and ectomorphy.

From the standpoint of clinical psychiatry, it cannot be said that this book offers any material which has not already been in general use in psychiatric circles beginning with the work of Kretschmer. It rests on sounder statistical basis. The authors' description of the sixty traits included under the three headings is excellent. They discuss the possibility of constitutional change without coming to any definite answer, but express the opinion that the manner of expression of a temperament can be modified, hinting that this is the purpose of "civilization."

Lest the charge be raised that constitutional psychology is a fatalistic thing, the authors state:

The aim is to develop every individual according to the best potentialities of his own nature, while protecting him from the fatal frustration of a false persona and false ambitions. This is not fatalism, but naturalism. Its end result is to increase, not decrease the individual's opportunities for accomplished living.



PSYCHIATRY IN MEDICAL EDUCATION.

By Franklin G. Ebaugh and Charles A. Rymer. *The Commonwealth Fund, New York; Oxford University Press, London.* \$3.50. 9½ x 6½; xxiv + 619; 1942. This book is the result of a survey made by the authors

to obtain a "factual picture in the United States of psychiatric teaching and of its progress, especially during the last decade." It attempts "to give an unbiased view of the present situation with regard to the content of the curriculum, the method of teaching, and the general status of psychiatric education." The completed volume represents an enormous amount of labor in the assembling of the data and painstaking care in bringing the work to fruition. Much of the material was furnished by a survey made in 1931-1932 of the psychiatric teaching in 66 medical schools in the United States and two in Canada. Additional data from questionnaires, reports, articles, letters, personal communications and conferences have rounded out the report.

The chief value of the volume, aside from the general picture which it presents of the growing recognition of the importance of psychiatry in the teaching and practice of medicine, is its usefulness as a reference work for deans of medical schools and heads of departments of psychiatry. It furnishes information not only on the types of courses in psychiatry and method of presentation but on the teaching activities in psychiatric hospitals and the opportunities for postgraduate work in different institutions. Undoubtedly it will stimulate many of those schools that are lagging in their program in this field and it will also act as a check where enthusiasm has led to over-development along certain unproductive lines.

In a Foreword, Adolph Meyer says:

Dr. Ebaugh and Dr. Rymer offer a synthetic as well as regional accounting with a real integration of the programs influencing not only the specific departments of psychiatry but the permeation of the entire medical training with the most significant advance of twentieth-century medical training—the consideration and collaboration of the person of the patient and the social setting, and the penetration and coordination of the specialties which at times seem to threaten the perspective of the technical developments. The entire trend of medicine calls for a degree of mutual understanding between the branches of medicine of the patient as person, for collaboration of the physician in a program of health, and for the intensive study of the specific factors in the public and individual needs of treatment.



THE USE OF PERSONAL DOCUMENTS IN PSYCHOLOGICAL SCIENCE. *Prepared for the Committee on Appraisal of Research. Bulletin 49.*

By Gordon W. Allport. *Social Science Research Council, New York.* \$1.50. 9 x 6; xix + 210; 1942 (paper).

The materials of this excellent monograph are organized around three central topics, namely: (1) The use of personal documents; (2) The forms of personal documents; and (3) The value of personal documents in psychological research.

Under the first topic, the author has discussed the attitude of various eminent psychologists and psy-

chiatrists in the development of the trend of recognizing the importance of personal documents in psychological research. The list of purposes in which such material has been profitably used covers such a wide range of theoretical, practical, historical, and methodological interests that the field is certain to develop rapidly with sustained study and continued improvement.

The values, as well as the dangers encountered in the use of each of the various forms of personal documents (autobiographies, questionnaires, verbatim recordings, diaries, letters, and personal expressions in the form of literature, art, music, etc.) are discussed under the second heading, and the need for further research is emphasized.

A critical evaluation of the use of personal documents in psychological research makes up the third and last section of the work. The case both for and against the use of personal documents is strongly argued in an attempt to reach a common sense, middle-of-the-road attitude which will be conducive to critical, yet careful and sympathetic work.

In conclusion, the author makes a plea for more bold and radical experimentation with personal documents; lists the pitfalls of which the workers in the field must continuously be aware; and suggests strong counter measures against the theorists who hold that personal documents are of little or no value in psychological research.

The work is well documented, listing a bibliography of some 200 titles, and carries indices of names as well as subjects.



PERSONALITY AND MENTAL ILLNESS. *An Essay in Psychiatric Diagnosis.*

By John Bowlby. *Emerson Books, New York.* \$2.75. 8 x 5½; viii + 280; 1942.

Bowlby's purpose in presenting his work in a somewhat incomplete state is in "the hope that it may stimulate others to undertake the research necessary to confirm or to modify my conclusions." His observations "confirm in principle a certain theory of typology, dispose of many common beliefs and suggest a new basis for the classification of the psycho-neuroses. . . . An attempt has been made to review all the clinical material published in English, to collate it and to compare it with new observations." The "gradation theory" is accepted by the author. No attempt is made "to discover hard and fast lines dividing healthy personalities which we meet with daily in our ordinary lives, personalities stricken with neurotic symptoms and those people whose personalities have been completely deranged, whether temporarily or permanently, by psychotic changes, because it is believed that no lines exist." The author holds that a knowledge of the *total personality* traits furnishes a more satisfactory method

for classification and diagnosis than an appraisal on particular symptoms.

The method of presentation of the material is as follows: (1) An examination of the work which has already been done in studying personality and relating it to neurosis and psychosis; (2) a schedule of personality traits which the author regards as significant in distinguishing the major types of personality; (3) tabulation of these traits for 36 patients who have suffered from a psychosis; (4) isolation of 33 traits which are believed to have special significance for diagnostic purposes; (5) description of certain personalities which are regarded as typical of certain groups of unstable personalities; (6) tabulation of the traits for another 29 patients suffering from neurotic symptoms; (7) tentative conclusions as to the relationships of certain personality types to neurotic and psychotic syndromes and suggestions of some revision of the present grouping of the neuroses.

This is a stimulating and thought-provoking book. It contains much clinical material that will be useful to the psychologist. In two appendices are given (a) the specificity of 33 schizoid traits and (b) 72 non-specific traits. There is a bibliography of 79 titles and a useful working index.



COMPANION DOG TRAINING: A Practical Manual on Systematic Obedience; Dog Training in Word and Picture.

By Hans Tossutti. Orange Judd Publishing Company, New York. \$2.00. 7½ x 5½; 226; 1942.

The author of this book does not advocate that the extension of one of the rules of our public school system, namely the compulsory training of children up to a certain age, be applied to dogs, but those who read his book understandingly, or, indeed, those who are aware of the fine results obtainable in careful dog training, can appreciate what a rule of this kind would mean—not only to dog owners and their neighbors but to the animals themselves. Perhaps it will be in this direction that the S.P.C.A. will next bend its efforts!

Tossutti has had wide experience in dog training both in Europe and in this country. He emphasizes the importance of *knowing how to teach individuals how to train dogs*. Not all dogs are equally satisfactory for training: some breeds are better fitted, temperamentally, than others, yet all dogs, if carefully and sympathetically handled will yield to some kind of schooling.

The first five chapters of the present book serve to give the reader a general viewpoint concerning the psychology of dog training, equipment needed, praise and punishment, puppy education, and obedience. Then follow 12 lessons, each one dealing in detail with some one phase in schooling. The last seven chapters deal with more advanced work such as obedience tests, trailing or tracking, and correction of bad habits. Many illustrations are included in the text and the

volume is provided with a brief but comprehensive index.

The volume will be especially welcomed by those dog owners who are so situated that they are unable to attend the training classes which are being established in increasing numbers in the larger towns and cities in this country.



CONTRIBUTIONS TO A PSYCHOLOGY OF BLINDNESS.

By Samuel Perkins Hayes. American Foundation for the Blind, New York. \$2.50. 9½ x 6½; viii + 296; 1941.

This is a comprehensive treatise on the problems in the psychology of blindness, disposing of the fiction of the vicariate sensory compensation, and an excellent résumé of the thought and experimental work on "facial vision" or the sense of obstacles, which seems finally to be the result preeminently of auditory discrimination and to a lesser extent perhaps of tactual perceptions. Blind children are shown not to have any superior memory, and the presence of superiority is related to a special interest in the subject matter. There is also evidence that schools for the blind are not getting poorer mental material than was the case before blindness from birth infection was sharply reduced.

The second part of the book has to do with the adaptation of test materials for use among the blind in the study of special psychological assets. One gets from this review a hint of very serious difficulties which the handicap of blindness imposes on testing methods. Particularly important is the slowness with which blind subjects read. In a study of the influence upon school success of the age at which vision was lost, no positive correlations were established.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SCIENCE AND SANITY. An Introduction to Non-Aristotelian Systems and General Semantics. Second Edition.

By Alfred Korzybski. Science Press Printing Company, New York. \$6.00. 9½ x 6; lxxi + 806; 1941. The first edition of this work appeared in 1933. Since then such advances have been made in Semantics that a revised edition has become inevitable.

It is interesting to contrast this voluminous work with Hayakawa's brief essay *Language in Action* recently reviewed in these columns. The latter writer adheres closely to his text and gives us a highly concentrated solution of Semantics, yet without ever using that term; Korzybski, on the other hand, employs the word frequently but dilutes his discussion with extraneous matter whose relation to the discipline usually associated with the author's name seems somewhat

remote. A peculiar diffuseness of literary expression is the result. Some critics may take exception to this but the average reader who may have only the haziest idea as to what Semantics is all about is likely to find the resultant digressions refreshing.

A clue to the explanation of this form of writing is to be found in Korzybski's own definition of Semantics: "the application of some methods of exact science to the solution of human problems." Such a definition is sufficiently broad to cover practically every field of learning, and the crowded entries in the 18-page index seem to indicate the desire of the author to effect just such a coverage. Korzybski has an encyclopedic mind that recalls that of Karl Pearson, who expanded the last edition of the *Grammar of Science* in the same way. Like Pearson, Korzybski is quite at home in the theoretical abstractions of such scholars as Planck, Einstein, Minkowski, Morgan, Jung, Veblen, etc. (Strangely enough, the name of that almost universal genius, Forel, is lacking from the bibliography of 619 items.)

To the present reviewer it appears that in some respects his work merits adverse criticism. In order to economize on paper and ink (a worthy ambition in these days) the author has had recourse to multitudinous abbreviations, which impede the reader's effort to get the drift of the author's thought. For instance, the term "non-aristotelian" is represented by a capital A surmounted by a macron, and the familiar "etc." gives ground to a combination of punctuation marks whose extensional meaning is likely to evade the reader. It is true that most of these abbreviations are explained in the text, but the explanations are buried in one of the earlier chapters where they are difficult to find when needed.

It is something of a shock to find the ambiguous expression "and/or" sprinkled so lavishly through these pages. These words have different meanings, and the device of so combining them is frequently resorted to by writers who are either uncertain as to which one they mean, or who do not wish to commit themselves irrevocably to either possibility. Neither of these explanations apply here.

Finally, it must be remembered that printed marks on a page are merely symbols of spoken words addressed to the ear, which can apprehend them only one at a time. The meaning of vocal sounds depends on the order in which they are apprehended, and the printed symbols must follow the same order if they are to convey the same meaning. (Our practice of saying "eighteen" and writing "18" is not an exception, for "18" is not a phonetic but an arithmetic symbol.) A monodimensional scheme is not adequate to the complexity of Korzybski's thoughts, and he finds it necessary to introduce at times a vertical relationship in addition to the more familiar horizontal one between pairs of words. His symbols are addressed to the eye, not the ear, consequently the book should not be read aloud, and is not intended to be. The author is of

course the best judge as to how his thoughts may be most clearly represented on the printed page, but in this case he has resorted to a device among whose results is an inevitable increase in esotericity.

Finally, a word is needed to explain why vengeance for the evils of modern civilization should be visited on Aristotle. The philosophy of Aristotle is essentially one of dichotomy. The universe consists of such opposed entities as motion and rest, force and matter, time and space, and body and soul. But modern physicists tell us that motion and rest are relative, not mutually exclusive, states; that force and matter are merely manifestations of a single underlying reality; that time and space are not separate continua but different dimensions in the same continuum; and while the synthesis of body and soul cannot yet be demonstrated it may be accepted as an article of faith. One wonders what the response of the Stagirite would be if he could read this book.



THE BOYLSTON STREET FISHWEIR. *A Study of the Archaeology, Biology, and Geology of a Site on Boylston Street in the Back Bay District of Boston, Massachusetts. Papers of the Robert Peabody Foundation for Archaeology. Volume II.*

By Frederick Johnson in collaboration with Henry C. Stetson, Frances L. Parker, William J. Clench, and others. Published by the Foundation, Phillips Academy, Andover, Massachusetts. \$2.00. 9½ x 6½; xii + 212 + 13 plates + 1 folding map; 1942 (paper). It is pointed out in the introduction that the term "fishweir" can only be used as a convenient name for this assemblage of vertical stakes and horizontal brushwood" found in an area of about two acres lying roughly 30 feet below the present level of the Back Bay region of Boston. The top 18 feet of the area consists of sand and gravel added between the years 1856 and 1894 to fill in the marsh and mud flats of the Charles River. The next 13 feet consists first of a top layer of peat, then a layer of silt, a shell layer (4½ feet below the upper peat layer), more silt, then at a depth of 13 feet another shell layer in which first appear the tops of the stakes of the Fishweir. At varying levels below this—2 to 5 or more feet—is found a lower peat layer and an underlying bed of blue clay in which the lower ends of the stakes are embedded.

That the Fishweir was built by human hands there can be no doubt; also, that it was built when the sea level was considerably below its present level there can be no doubt. It is estimated that more than 50,000 stakes, sometimes placed in groups and sometimes singly, with horizontal bundles of brushwood forming the side walls, were used in its construction. At present no attempt to place the date of the construction of the Fishweir is made but from certain evidence it is quite possible that it was built sometime previous to 3,000

B.C., at about which time it is estimated that the land commenced to submerge. The presence of the Fishweir first became known in 1913 when excavations were being made for the Boylston Street Subway.

The present study is divided into three parts: (1) The excavation of the Fishweir; (2) Analysis of materials from the building excavation. This includes mechanical analysis of the sediments and the identification of foraminifera, mollusks, oysters, diatoms, identification and physical condition of the stakes and wattles of the Fishweir, chemistry of ancient beech stakes, pollen analysis of the lower peat layer and of the silt, and the tentative dating of the deposits; (3) A discussion of the implications and significance of the data from the building excavation.

The text is accompanied by many fine photographic plates illustrating details of the excavations, microscopic examinations of stakes, diatoms, pollen, etc., and figures showing geological deposits, plan of Fishweir, and pollen profiles. Much data is given in tables concerning the occurrence of different species of plant and animal life in the sediment and in an appendix the construction of modern fishweirs is discussed in order to throw light on this ancient structure. (Modern techniques in the study of ancient wood have so far advanced that Baily and Barghoorn, in their discussion of the stakes and wattles of the weir find good evidence for their statement that "the weir appears to have been constructed and repaired during the spring.") A bibliography of 67 titles is also included.



SCIENCE FOR THE PROSECUTION.

By Julius Grant. Chapman and Hall, London. 15s. net. 9½ x 5½; vi + 302; 1941.

This is a semipopular but nevertheless scholarly treatment of the methods used in criminological work. It will appeal to the intelligent general reader, the lawyer, and those having to do in a professional way with physics, chemistry and pathology. Each chapter is provided with a reading list for those who wish more information on any particular phase of the subject.

Grant has provided an interesting introductory chapter on the scientific approach to crime in which he discusses forensic science laboratories in England and the need for a National Medico-Legal Institute.

Minor criminals however, have minor objectives; it is the major criminals who hunt the biggest game, and their methods are entirely different. From the scientific point of view they may be specialists in their own sphere, and by continual study they may so perfect their technique as to become the foremost experts in the science of their own particular 'line'. Such cases therefore, must be dealt with by experts of equal standing on the other side of the fence, and in the past at any rate, it has not infrequently happened that such counter-experts have not been immediately available.

Nearly a third of the book is devoted to a discussion of optical methods of investigation with special chapters on ultra-violet rays, infra-red rays, spectroscopy, X-rays, and the microscope and camera. Combinations of these methods frequently yield remarkable results, as in the following example: fibres of certain paper appear identical when examined under the microscope or when stained or treated by chemicals. However, the use of filtered ultra-violet light in conjunction with the microscope will make it possible to ascertain whether the same combination of fibers is used in one paper as in another.

No attempt has been made to deal exhaustively with chemical methods in use in criminology but an interesting general discussion of the subject is given and many examples of crime detection are explained. The section on blood group tests and serum analysis gives the latest results in this field of research and define clearly the uses and limitations of the tests in problems of heredity and disputed paternity. Finally, the rôle of the psychologist in criminology is discussed. The author here is thoroughly aware of the opportunities which are opening up in this field of approach and many of the attendant difficulties. It is his belief that an important rôle for the psychologist is in the advice which he may give as to the nature of the punishment, this being based on a study of the mentality of the offender rather than the crime which he committed.



THE HISTORY AND EVOLUTION OF SURGICAL INSTRUMENTS.

By C. J. S. Thompson with a Foreword by Chauncey D. Leake. Schuman's, New York. \$8.50. 10½ x 6½; 113; 1942.

This interesting survey, by the curator of the Royal College of Surgeons, is based on the collection of surgical instruments that had been accumulated within the halls of the institution's building. This structure was largely destroyed by Nazi bombing in the spring of 1941 and little now remains of the once priceless collection of instruments. Fortunately some accounts had previously been published and Thompson had already prepared much of the present volume, so that there is now preserved a complete record of the famous collection which depicted in so remarkable a manner the development of the technique of surgery from the earliest known records down to modern times.

It is not until the Roman period, at the beginning of the Christian era, that the actual instruments used by surgeons are found. Chiefly we know of the instruments of earlier periods through descriptions given by classical authors and representations in marble and stone. The earliest known representation of the scalpel is on a sculptured tablet of stone (date probably 300 B.C.), yet Thompson says that "the cutting knife or scalpel... was probably the earliest instrument used

by the surgeon." Roman scalpels frequently embraced two instruments in one—a scalpel at one end and a scoop or spoon at the other. They were usually entirely of metal and the "handles of some of the Roman instruments are often finely worked and occasionally damascened with silver." Handles of wood and bone appeared about the 14th century. After Lister's time the all metal surgical instrument returned.

In the first century of the Christian era we have the first description, by Aulus Cornelius Celsus, of the amputation of a limb. The knife, judging from specimens found at Pompeii, was probably like a large scalpel with a steel blade and bronze handle. Many illustrations are given in the book of amputation knives, from the early straight blade through a whole series of curved (concave and convex) blades to the time of Liston (1794–1847) who established the use of the long straight blade (14½ inches long and 1½ inches deep). Although the saw as used in surgery passed through many different types "no radical change has been made in the saw used in amputations, and it still remains very similar in shape to the tool employed in ancient times."

In addition to the chapters on the scalpel, the amputation knife, and the saw, there are sections on the trepan, vaginal dilators and speculum, head saws, forceps (artery and dressing), bullet-forceps and extractors, instruments for phlebotomy and venesection, trocars, and operating tables. The volume is handsomely printed and illustrated and is provided with a general index.



THE MEN WHO MAKE THE FUTURE.

By Bruce Bliven. Duell, Sloan and Pearce, New York. \$2.75. 8½ x 5½; xiii + 325; 1942.

In this book, written for the general public, the author, a journalist not a scientist, sets out to demonstrate that the scientists more than any other group are the men who make the future and are in a position to rescue civilization, if they only will. Why, he asks, has the body of scientific knowledge, for all the changes it has wrought in the fabric of everyday life, thus far made so little impression on the course of human destiny? It is suggested that a beginning of the application of science to the affairs of the world be made even if it is on a small scale only.

The material for the book was acquired by visiting numbers of research laboratories all over the country and interviewing people actively engaged in various kinds of research. While the greater part of the book is concerned with giving a survey of the more recent and exciting discoveries in the fields of genetics, physiology, chemistry, physics, astronomy, medicine, etc., considerable attention is given to the men themselves and their attitudes towards civilization and its problems.

Mr. Bliven states that he found the scientists on the whole rather optimistic regarding the future. They

do not believe that civilization is perishing but rather on the threshold of a new and better existence. Men must soon realize how foolish it is to kill each other for the acquisition of raw materials and natural resources which can be produced easily and abundantly in the laboratory. In one chapter we are given a glance at this world of tomorrow when the many products of the laboratory are brought into the practical realm of every day life.

The book is written in an interesting style and should appeal to the layman interested in the achievements of science but who neither has the time nor the technical knowledge required for reading the many scientific periodicals. Portions of the book have already been published in the *New Republic* and *The Reader's Digest* and have no doubt been widely read.



AN ENGLISH 13TH CENTURY BESTIARY. *A New Discovery in the Technique of Medieval Illumination.*

By Samuel A. Ives and Hellmut Lehmann-Haupt. H. P. Kraus, New York. \$1.85. 10½ x 7½; 45 + 8 plates. 1942.

The subject of this book is a Latin manuscript copy of *Physiologus*, now the property of H. P. Kraus of New York. Its illustrations have been pounced.

Pouncing was a method of mass production of illustrations before the invention of printing. The illustration to be pounced was perforated by pin pricks along the lines of its pattern, and then placed against white parchment. Powdered charcoal was then rubbed over it, penetrating the perforations and so transferring the design to the parchment.

The pin pricks in the pattern of each illustration perforate through the following illustrations, indicating the pouncing was done after the book was bound. Since each illustration bears the pounce marks of the previous ones, it follows that the reproductions could not have been made directly from the originals, but that the pounced copy was the master stencil. The application of charcoal would have ruined the hand-colored illustrations, and the latter show no indications whatever of such treatment.

The text pages are not perforated, which seems to indicate that they were not part of the book when the pouncing was done. The present binding is therefore not the original. The author's study has led him to believe that the binding dates from the 15th century, the text from the 13th, and that the illustrations are still older, and were separately bound when the pouncings were made.

Photographic reproductions of some of the original figures and of one page of text add much to the interest and value of this work, which consists of a description of the original manuscript and a discussion of its probable lineage and its relationship to 16 other *Physiologus* manuscripts.

ADVENTURES IN SCENERY. *A Popular Reader of California Geology.*

By Daniel E. Willard. *The Jaques Cattell Press, Lancaster.* \$3.00. 9½ x 6½; 438; 1942.

This volume may be best classified as a popular reader of California geology. In it the author has gathered together the results of many scientific investigators, interpreted them and presented them in a non-technical form simple enough to interest the general reader. Geology of the western coast, not only of California but of adjacent regions, lends itself easily to such popular treatment.

The story of California is complicated. The real history goes back through the geologic ages. All that is now before us is the product of what has gone before. The rugged mountains, the splendid canyon gorges, the gold washed from stream beds or dug from hard rock veins, the broad expanse of the great Interior Valley, the fields and fertile valleys in which are grown the marvelous variety of farm crops, fruits, vegetables, and nuts, . . . all are the product of the great geologic laboratory which is now called California. The geological story is long. Time has been long. California as we now see it is the product of a long past.

After a discussion of the principal geologic features and the processes involved in producing the varied coast line, mountains, valleys, deserts, fertile lands and the exceedingly varied climate, etc., the author in a section entitled "Geology from a motor car" devotes considerable space to a "Guide for tourists." Eight auto tours are outlined which take in most of the points of particular scenic interest.

The many photographs and drawings add interest to

the text. A bibliography, a glossary and an index are included.



SCIENCE AND MAN. *Twenty-Four Original Essays by Aleš Hrdlička, Reinhold Niebuhr, Jacques Maritain, Alfred E. Cohn, Arthur H. Compton, Harold C. Urey, et al.*

Edited, with an Introduction and Conclusion by Ruth Nanda Anshen. Harcourt, Brace, and Company, New York. \$4.00. 8½ x 5½; viii + 494; 1942.

Often during periods of upheaval, an uneasiness on the part of thinkers concerning the pass to which mankind has come is reflected in statements on the vagaries of human thought and in programs to set it on the right tract. It is not surprising, therefore, that the present volume should appear at this time. Twenty-four leaders in modern science have contributed original essays to a discussion of the place of science and its achievements in the world of man and have endeavored to point out the paths to be followed if science is to be man's servant rather than man's master.

Among the contributors are Aleš Hrdlička, the brothers Compton, the late Bronislaw Malinowski, founder of a school of the science of man, Julian Huxley, Walter B. Cannon, to mention a few of the more outstanding. The essays are divided into groups such as Science and the universe; Science and society; Science and internationalism; Science and the individual, etc.

An introductory chapter and a conclusion are contributed by the editor, Mrs. Anshen. This volume is the second in the Science of Culture Series. The book is well indexed.



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